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ADDITIONAL EVIDENCE OF MUTATION IN OENOTHERA[1]

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(WITH SEVENTEEN FIGURES)

Introduction

Much of the advance which has been made in genetics and practical breeding during the last decade has been a direct result of the promulgation by DE VRIES of the theory of the origin of species and varieties by mutation. That recessive Mendelian variations originate singly by mutation has been shown by several investigators, notably by MORGAN, who has observed the origin of more than 150 such variations in his cultures of *Drosophila*. Many opponents of the mutation theory deny, however, that progressive mutations ever occur in homozygous strains, or that true species, differing from the parent in several independent characters, have ever been observed to originate at a single step by mutation. DAVIS,[2] for example, is in accord with the mutationists in regarding *Oenothera gigas* as a marked progressive mutation of specific rank, but he denies that *Oenothera Lamarckiana*, the parent form of *O. gigas*, is homozygous. The facts (1) that *O. Lamarckiana* is not known as a native component of any flora, (2) that its known history has been that of a cultivated plant or an escape from cultivation,

[1] Published by permission of the Secretary of Agriculture.

[2] DAVIS, B. M., Cytological studies on *Oenothera*. III. A comparison of the reduction divisions of *Oenothera Lamarckiana* and *O. gigas*. Ann. Botany **25**:941–974. 1911. "*Oenothera gigas* is a progressive mutant, its peculiarities being clearly associated with the changes in its germ plasm incident upon the doubling of its chromosome number" (*op. cit.* p. 974).

and (3) that its habit of throwing off marked germinal variations is paralleled by the behavior of certain interspecific hybrids in the F_2 and F_3 generations seem to DAVIS[3] a sufficient indication that this plant is of comparatively recent hybrid origin, and that its mutations are due to germinal instability resulting from hybridization. He holds that the germinal variations of *O. Lamarckiana* and of various hybrids which he has studied show marked progressive evolution which seemingly cannot be accounted for on a Mendelian basis. Although he does not deny that slight discontinuous variations may occur in homozygous strains (and he insists that the term mutation ought to be used only for such variations), he is of the opinion that variations large enough to be of evolutionary significance occur rarely if at all except in heterozygous lines.

GATES[4] does not believe that *O. Lamarckiana* is a recent interspecific hybrid, but does ascribe its mutations to germinal instability caused by occasional random crossing with other types. In their main conclusion, that when germinal variation occurs it usually follows crossing, DAVIS and GATES appear to agree. GATES, however, is more emphatic than DAVIS in his conclusion that mutation in *Oenothera* is not merely a result of Mendelian redistribution of unit characters, but is a distinct type of variation. He believes, moreover, that mutation sometimes takes place in pure as well as in hybrid lines. Since the phenomena are identical in the two cases, he has laid especial stress on the fact that there is no excuse for confusing mutation, when it occurs in hybrids, with any type of Mendelian segregation.[5]

[3] DAVIS, B. M., Genetical studies on *Oenothera*. II. Amer. Nat. **45**:193–233. 1911; III. *Ibid.* **46**:377–427. 1912; IV. *Ibid.* **47**:449–476, 547–571. 1913.

[4] GATES, R. R., Mutation in *Oenothera*. Amer. Nat. **45**:577–606. 1911.

———, A contribution to a knowledge of the mutating *Oenotheras*. Trans. Linn. Soc. Lond. II. Bot. **8**:1–67. 1913.

———, Tetraploid mutants and chromosome mechanisms. Biol. Centralbl. **33**:92–99, 113–150. 1913.

[5] In this author's last paper he says: "The cytological evidence shows that germinal changes may and do occur which are independent of all the laws of hybrid combination and hybrid splitting. This generalization is of more fundamental significance than might at first appear; for it shows that mutation in *Oenothera* is a process *sui generis*, and that no amount of hybrid combination and splitting, Mendelian or otherwise, is sufficient to account for it." GATES, R. R., Breeding experiments which show that hybridization and mutation are independent phenomena. Zeitschr. Ind. Abstammungs- u. Vererbungslehre **11**:209–279. 1914.

HERIBERT-NILSSON[6] has made the first serious effort to explain the variations of *Oenothera Lamarckiana* on a strictly Mendelian basis. He does not hold with DAVIS that this species is necessarily of hybrid origin, but rather that it is a collective species, embracing a number of different strains which constantly cross among themselves. Consequently he assumes that the mutation phenomena do not exemplify progressive and regressive species formation, but merely the synthesis of new combinations from factors already existing within the species.

Although it is by no means true, as some critics seem to imply, that the mutation theory must stand or fall on the evidence derived from *Oenothera*, it must nevertheless be admitted that failure to find a parallel among other more fortunately chosen species of this genus to the mutation phenomena shown by *O. Lamarckiana* would discredit, if not invalidate, much of the direct evidence of mutation which has been so laboriously won by DE VRIES. DAVIS[7] has said that "it is evident that the adherents of the mutation theory are sensitive to the doubts freely expressed concerning the status of *Oenothera Lamarckiana*, the behavior of which in throwing off marked variants is cited as the most important evidence for the origin of species by mutations. . . . . Consequently, mutationists are likely to bring forward as rapidly as possible any evidence that may seem to indicate the appearance of clear inheritable variations of a marked character in forms of pure germinal constitution, i.e., in homozygous material."

It is the object of this paper to present additional evidence of mutation in *Oenothera*, derived from one of the small-flowered, self-pollinating wild American types. Before proceeding farther, however, it should be stated that a considerable body of similar evidence has already been obtained.

DE VRIES[8] and STOMPS[9] have twice observed the origin of a dwarf variety of *O. biennis* by mutation, once in a pure line of

[6] HERIBERT-NILSSON, N., Die Variabilität der *Oenothera Lamarckiana* und das Problem der Mutation. Zeitsch. Ind. Abst. u. Vererb. **8**:89–231. 1912.
———, *Oenothera* Problemet. Svensk. Bot. Tidskr. **7**[1]: pp. 16. 1913.

[7] DAVIS, B. M., Mutations in *Oenothera biennis* L? Amer. Nat. **47**:116–121. 1913.

[8] DE VRIES, H., Die Mutationen in der Erblichkeitslehre. pp. 28–30. 1912.
———, Gruppenweise Artbildung. pp. 299–306. 1912.

[9] STOMPS, THEO. J., Mutation bei *Oenothera biennis* L. Biol. Centralbl. **32**:521–535. 1912.

O. biennis var. *leptomeres*,[10] and once in a cross between this variety and typical *Oenothera biennis*, from which var. *leptomeres* itself doubtless arose by mutation. STOMPS has also described *O. biennis* mut. *semigigas* from the same culture of *O. biennis* var. *leptomeres*×*O. biennis* which gave rise to the dwarf. A recent letter from Professor DE VRIES (dated May 16, 1914) states that mutations from *O. biennis* are still being obtained at Amsterdam.

STOMPS[11] has just published a second report on mutations in *O. biennis*. He records the origin by mutation, in a pure line, of *O. biennis* var. *sulfurea* De V. (long known as a wild component of the Dutch flora), together with mut. *nanella* and mut. *semigigas*. GATES[12] has likewise announced the discovery of mutations (*O. biennis lata*, *O. biennis laevifolia*, *O. biennis rubrinervis*) from *O. biennis*, but has not yet published a full account of his cultures.[13] Finally, DE VRIES has obtained two different mutations, *O. salicifolia* and *O. salicastrum*, from wild seed of a strain of the self-pollinating *O. biennis* "Chicago" which he collected near Courtney, Missouri; and the writer[14] has given a preliminary account of *Oenothera stenomeres* mut. *lasiopetala*,[15] a hairy-petaled derivative of one of the small-flowered cruciate Onagras.

[10] *Oenothera biennis* var. *leptomeres* Bartlett. Amer. Jour. Bot. 1:242. 1914= *Oenothera biennis* var. *cruciata* De Vries, not T. & G.

[11] STOMPS, THEO. J., Parallele Mutationen bei *Oenothera biennis* L. Ber. Deutsch. Bot. Gesells. **32**:179–188. 1914.

[12] GATES, R. R., Parallel mutations in *Oenothera biennis*. Nature **89**:659–660. 1912.

[13] Since the above was written, an account of the cytology of *O. biennis* mut. *lata* has been received. See GATES, R. R., and THOMAS, NESTA, A cytological study of *Oenothera* mut. *lata* and *O.* mut. *semilata* in relation to mutation. Quar. Jour. Micr. Sci. **59**:523–571. 1914.

[14] BARTLETT, H. H., An account of the cruciate-flowered *Oenotheras* of the subgenus *Onagra*. Amer. Jour. Bot. 1:226–243. 1914.

[15] By an unfortunate oversight this name was published in Amer. Jour. Bot. as *O. stenopetala* mut. *lasiopetala*. The writer had originally used the name *O. stenopetala* for the species which was described as *O. stenomeres*. After the manuscript had been submitted to the editor, a change was made necessary by the publication of *O. stenopetala* Bicknell, Bull. Torr. Bot. Club 41:79. 1914. In one place the original name escaped notice and was not corrected. It is hoped that the error will not lead to any confusion.

It is shown in this paper (1) that the phenomena of mutation are as characteristic and as easily observed in one of the wild small-flowered self-pollinating Onagras as in *Oenothera Lamarckiana;* (2) that the mutations show characters unlike those of any other form with which the parent could have crossed; and (3) that the mutations cannot be ascribed to Mendelian segregation as at present understood. It therefore seems in the highest degree probable that mutation is a phenomenon which is independent of hybridization, and that the evidence of mutation which DE VRIES has found in *Oenothera Lamarckiana* is just as valid as though that species were known as a wild plant and not suspected of having had a horticultural origin.

Differential germination

Several of the most interesting mutations which were observed during the season of 1913 were found quite by chance. One lot of potting soil, in which the seeds of several strains were sown, proved to be a very stiff clay on which a hard crust formed. Germination was so poor that in several cases less than a dozen seedlings resulted from sowing perhaps a thousand or more seeds. It was afterward found that the seeds showed the usual percentage of germination when sown in good soil. In three different species the small progenies obtained when the seeds were planted under unfavorable conditions disclosed striking mutations, which had survived as a result of differential or selective germination. These mutations might easily have been overlooked in a seed pan containing several hundred seedlings, of which only a few were to be retained and grown to maturity.

The three mutant species were from widely separated localities. The seeds of one, from Plymouth, Massachusetts, were sent by Professor B. M. DAVIS; the others were collected by the writer at White Sulphur Springs, W.Va., and Lexington, Ky., respectively. The mutations of the two former species were lost before they matured. It will be useless, therefore, to give an account of their characters or of the cultures in which they appeared until they shall have been found again. In the case of the third species,

O. pratincola, the mutations were brought to maturity and have yielded a second generation. This species, therefore, has been systematically examined for variations, with the results recorded in this paper.

The Oenothera population at Lexington, Kentucky

During a brief visit in October 1912, the writer was able to find only two species of *Oenothera*×*Onagra* at Lexington, Ky. They are both new and are referred to below under the names *O. pratincola* and *O. numismatica*. If any other species occur within two or three miles of the city, they must be very scarce. Of course, in October many plants were through blooming and not in such condition that any differences among them would show to the best advantage. Nevertheless, it is believed that no common species could have been overlooked. Nine seed collections were made from individual plants, which showed as great a range of variation as possible. These plants, and the strains descended from them, have been designated by letters from A to I. Eight of the strains proved to be taxonomically identical and are referred to as *O. pratincola*. Lexington A, B, and C were collected in a pasture near Town Creek, 2 miles west of Lexington, where they grew within 200–300 feet of each other. Lexington E, F, G, H, and I were collected at random in vacant lots and within a mile of the city on the west. Lexington D is the only strain of the 9 which is referred to *O. numismatica*. The parent plant grew by a roadside about 2 miles east of Lexington. In addition to the seed collections, many rosettes were collected which flowered in Washington in 1913. Thirteen plants from the same general region as plants E to I proved on flowering to be typical *O. pratincola*, as were also 26 plants from the edge of a field near the reservoir east of the city. It thus appears that *O. pratincola* constitutes the bulk of the *Oenothera* population at Lexington. *O. numismatica* is much scarcer; it did not occur at all among the rosettes which were collected, and was seen in flower only east of Lexington.

The salient characters of the two evening primroses obtained at Lexington are the following:

In *O. pratincola*	In *O. numismatica*
A well-grown plant, is 1.5 m. high, and loosely branched.	A well-grown plant, is about 1 m. high, and densely branched.
The basal branches are frequently simple.	The basal branches bear tertiary branches and resemble the main stem.
The flowering time lasts about six weeks.	The flowering time lasts only about two weeks.
The lax terminal spike often becomes 5–6 dm. long (see fig. 1).	The dense terminal spike is about 2 dm. long in fruit (see fig. 2).
The lateral branches below the terminal spike are few in number and become 4–5 dm. long.	The lateral branches below the terminal spike are numerous and are seldom over 2 dm. long.
The lowest bracts of the upper lateral spikes are ovate, and grade upward to lanceolate.	The lowest bracts of the upper lateral spikes are nearly orbicular and grade upward through oblong to lanceolate (see fig. 2).
The calyx segments are so sparsely pilose as to appear practically glabrous.	The calyx segments are closely and finely pubescent.
The hairs of the calyx segments are about 1 mm. long, thick-walled, acute, with multicellular tuberculate bases.	The hairs of the calyx segments are less than 0.5 mm. long, and belong to two types: (1) an acute thick-walled type without tuberculate bases, and (2) a thin-walled, round-ended, clavate or cylindrical type.

Technical diagnoses of these two species, together with a discussion of their possible relationships, have been published elsewhere.[16] *O. pratincola* appears to be a frequent plant in the North Central States. *O. numismatica*, on the contrary, is known only from Lexington and may well be a local species, possibly derived by mutation from *O. pratincola*. Its close resemblance in certain characters to one of the mutations of *O. pratincola* is pointed out elsewhere in this paper.

The mutations of "Lexington C"

Seeds from four of the parent plants of *O. pratincola* which had been selected at Lexington were planted early in the spring of 1913.

[16] BARTLETT, H. H., Twelve elementary species of Onagra. Cybele Columbiana 1:37–56. 1914.

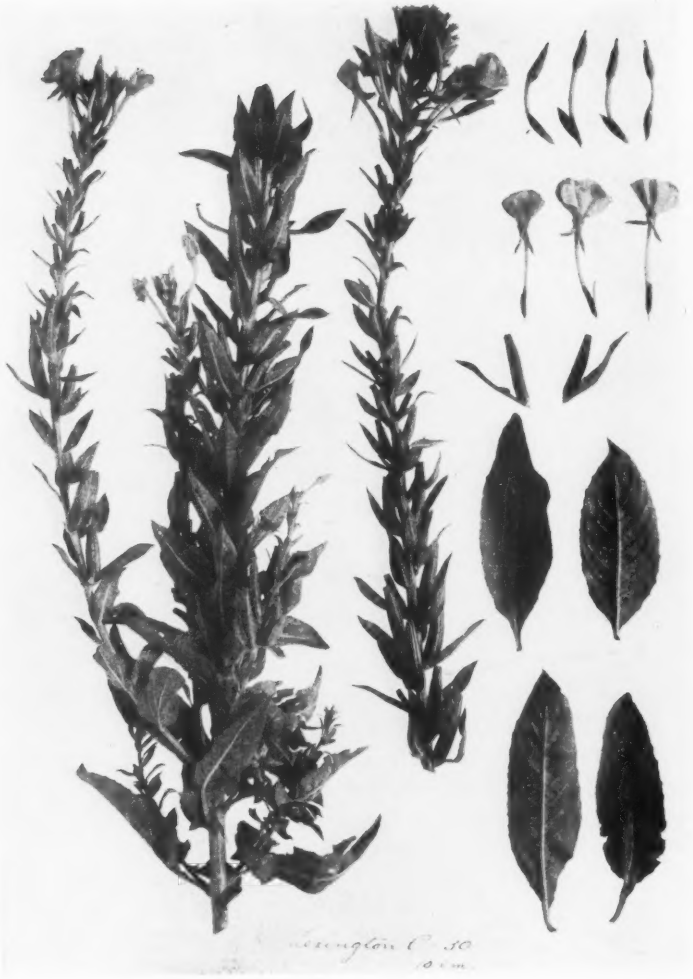

FIG. 1.—*Oenothera pratincola*, sp. nov.: upper part of main stem of Lexington C-30; leaves from middle of stem; flowers and buds; $\times\frac{1}{3}$.

FIG. 2.—*Oenothera numismatica*, sp. nov.: upper part of main stem of Lexington D-29; leaves from middle of stem; lateral branches from just below the terminal spike; characteristic foliage of such a lateral branch; in contrast with fig. 1, note the denser shorter spikes, which are only in flower a short time, the much closer branching, and the characteristic suborbicular leaves of the uppermost lateral branches; $\times\frac{1}{3}$.

Lexington A, B, and E germinated readily. Since no variation was noticed among the hundreds of seedlings of these three strains, all were discarded except 30 of each, which were potted off for the field cultures. The seeds of Lexington C, however, had been planted too deeply in unsuitable clay soil, and, although the seed

FIG. 3.—F_1 progeny of *Oenothera pratincola:* four of the 9 seedlings which constituted the first culture of Lexington C; the 2 upper plants, Lexington C-1 and C-2, are mut. *nummularia;* the latter bore seeds which gave rise to the F_1 culture referred to in table I; the 2 lower plants are typical *O. pratincola.*

pan received the same treatment as the rest, weeks passed before any seedlings appeared. At length 9 plants were obtained which were potted off. Almost from the first, they showed remarkable variation among themselves. Six (nos. 3, 4, 5, 6, 8, and 9) were typical *O. pratincola*, and agreed in all characters with the seed-

lings of Lexington A, B, and E; one (no. 7) was of a darker green color than the type, the leaves were somewhat narrower, and the petiole and midrib below the middle of the blade were particularly broad and white; two (nos. 1 and 2) had almost orbicular leaves, and constituted the most striking deviation from the expected form

FIG. 4.—F_1 progeny of *Oenothera pratincola*, Lexington C: the same plants shown in fig. 3, but a month older.

that the writer had ever observed in a seedling of *Oenothera*. In fig. 3 the two upper plants are the round-leaved variations, nos. 1 and 2; the two lower are typical *O. pratincola*, nos. 3 and 4. In fig. 4 the same 4 plants are shown when a month older. The reader will observe that the orbicular seedling leaves of nos. 1 and 2 have

been superseded in the more mature rosette by leaves of a different form, but that the sharp distinction between the variation and the typical form has not been obscured. The occurrence of so interesting a variation in Lexington C led to a careful examination of the strain for evidence of mutability.

A second sowing of the same seed on good soil resulted in a progeny of 720 seedlings from 1000 seeds. As soon as the seedlings were well rooted, they were transplanted to square seed pans in which they were widely enough spaced to allow of unimpeded growth for a month or six weeks. This system was followed in all subsequent work. Of course, the seeds were invariably sown on sterilized soil. After the seedlings were transplanted, the pans were frequently examined for mutations, and all plants which were noticeably divergent from the mass of the culture were marked for preservation. Among the 720 seedlings of the second sowing, there were only 4 round-leaved plants. Since the mass of the culture was uniform, and the round-leaved plants constituted an absolutely discontinuous variation from both the typical form and one other pronounced variant which occurred in the culture, it was concluded that they were probably mutations. In the following pages the round-leaved type is called *O. pratincola* mut. *nummularia*.[17]

In order to show the discontinuity between typical *O. pratincola* and mut. *nummularia*, photographs of two of the seed pans in which this mutation occurred are reproduced as figs. 5 and 6. At the time the pans were photographed, the plants were about as far advanced as nos. 1–4 in fig. 3. Comparison of the figures will

[17] The writer has suggested (Amer. Jour. Bot. 1:237. 1914) that mutations of experimental origin be given trinomial names such as *O. pratincola* mut. *nummularia*, in order to avoid confusion with names which must be given consideration in floristic works. A trinomial nomenclature has the advantage over the binomial system proposed by GATES (Trans. Linn. Soc. London II. Bot. 8:10. 1913) in that the parallelism of mutations occurring in different species may be indicated by the use of the same mutational designation. For example, a convenient way to show the parallelism between the mutations of *O. Lamarckiana* and those of *O. biennis* would be to call them *O. Lamarckiana* mut. *semigigas*, *O. biennis* mut. *semigigas*, etc. The trinomial used in this way need imply nothing as to the specific, varietal, or formal rank of a mutation, but only the manner of its origin. Nevertheless, for the sake of avoiding confusion, it would be well not to give any mutation a name which had previously been used in any subspecific category within the species which had given rise to the mutation.

show the complete identity, at this stage of growth, of different individuals of mut. *nummularia*, and also the great uniformity of the typical plants of the culture.

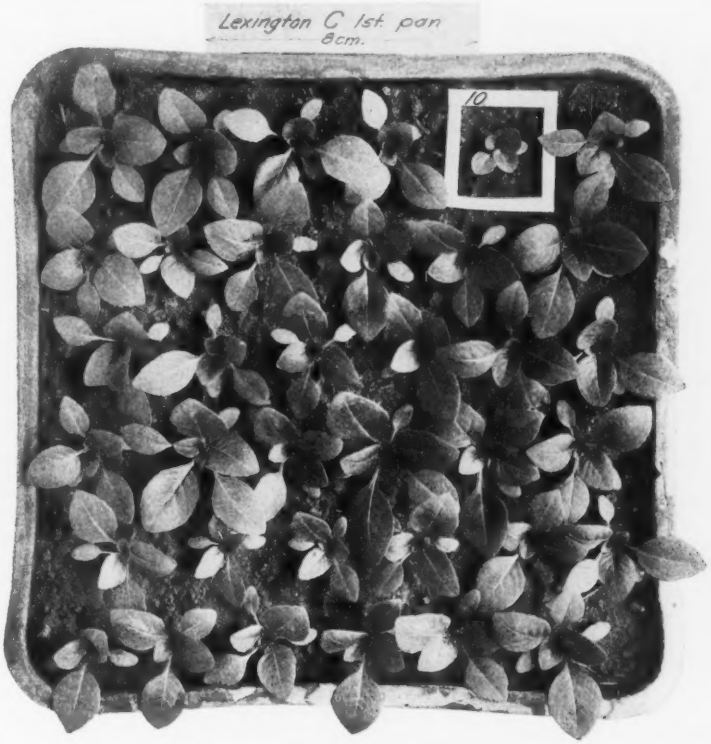

FIG. 5.—F_1 progeny of *Oenothera pratincola*, Lexington C, pan 1: the only mutation shown is Lexington C-10, mut. *nummularia;* the other plants are typical *O. pratincola;* about the same age as the plants shown in fig. 3.

In addition to the 4 plants of mut. *nummularia* which were discovered in the second sowing, there were solitary specimens of each of two other mutations, one plant (no. 12) like no. 7 of the first planting, and another (no. 18) unlike anything else in the culture. No. 18 had exceedingly narrow, red, subulate seedling leaves and

was called on this account mut. *subulata*. There were also 7 plants (nos. 13–16, 19, 20, and 22) which developed very slowly and were retained in the expectation that they might prove to be dwarfs, although there was no character but size to distinguish

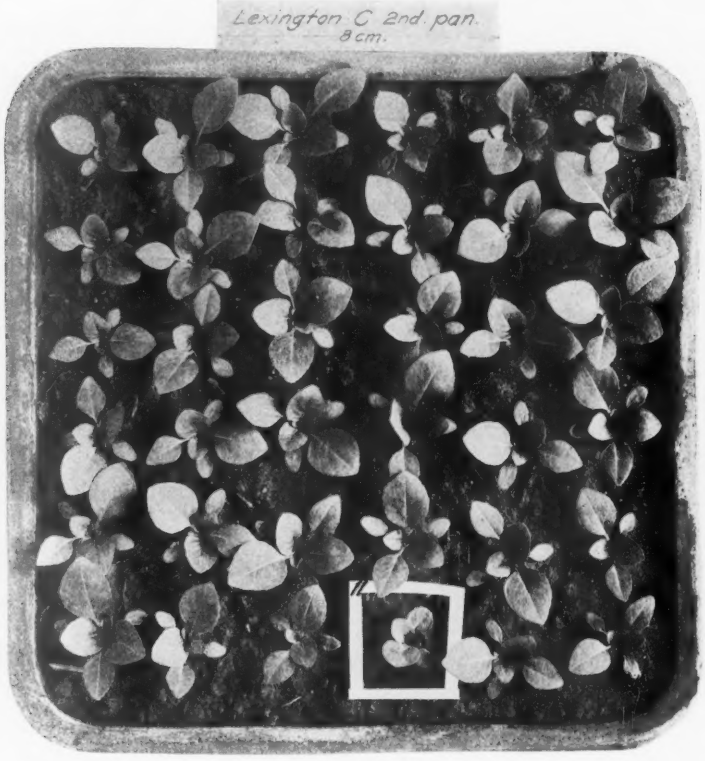

FIG. 6.—F_1 progeny of *Oenothera pratincola*, Lexington C, pan 2; the only mutation shown is Lexington C-11, mut. *nummularia;* the other plants are typical.

them from typical sister plants. The solitary plant of mut. *subulata* died, but the type has since been found to be one of the most frequent mutations of *O. pratincola*. The type represented by nos. 7 and 12 was designated as mut. *pusilla*. Its rosettes were about 4 cm. in diameter at maturity. The stem leaves were

linear-lanceolate. The stems were simple. No. 7 died just before flowering, when only 7 cm. high. No. 12 flowered at a height of 10 cm. The ovary was 7 mm. long; hypanthium 10 mm. long; calyx segments 4 mm. long, excluding the distant free tips, which were 1 mm. long. The calyx differed from that of the typical form not only in having distant calyx tips, but also in being densely soft-pubescent. Unfortunately, this plant was sterile and produced no seeds. As far as the writer is aware, mut. *pusilla* represents the extreme of nanism in the subgenus *Onagra*.

With a single exception, the 7 suspected dwarfs developed as quite normal plants, indistinguishable from the mass of the culture. One plant, no. 19, differed from the rest in that it had stiff, distant calyx tips 5 mm. long which were continued on the angles of the squarish bud as a marked carina. The buds were almost glabrous, as in the type form of the culture, but in marked contrast to some of the other mutations. This plant was self-sterile, but produced abundant seeds when pollinated with typical *O. pratincola*.

The Lexington C culture which was grown to maturity in 1913 included, besides the 9 plants from the first sowing and the mutations and suspected mutations of the second sowing, all the plants from two pans in which there appeared to be no variation. There were 72 of these plants, nos. 23–94.[18] When they matured two mutations were found which had not been detected in the early seedling stages. With these two exceptions, the plants were absolutely uniform among themselves, and exactly the same as Lexington A, Lexington B, and Lexington E. (Of each of these three strains 30 plants were grown to maturity.) The two mutations were not alike and were different from any of the other new types which had been obtained. Both, however, were almost

[18] The culture numbers of these plants are all given here in order to avoid lengthy repetition in subsequent papers which will deal with the same strains. It may be well to explain that every plant in the writer's garden is designated by the name of the strain (for which a number has often been substituted) followed by a succession of numbers which indicate the pedigree and number in the culture of each individual. Subscripts are used when it is wished to distinguish between sister plants grown in different years, or to indicate the years in which the successive generations were grown. "Lexington C-11_{13}," for example, would be the complete designation of the plant of mut. *nummularia* which is shown in fig. 6. Plants of the F_2 generation, grown in 1914, would be "Lexington C-11_{13-14}," "Lexington C-11–2," etc.

self-sterile. No. 28 was half as high as typical plants of the culture; the leaves were broader and white-margined; the buds were smaller and closely viscid-puberulent with a hair type which does not occur in the typical form; the branching differed in that there

A B

FIG. 7.—A, *Oenothera pratincola* mut. *nummularia*, Lexington C-21; B, *Oenothera pratincola* (typical), Lexington C-16; the 2 plants are of the same age and were grown under identical conditions; note particularly the difference in the branching.

were numerous inflorescence-bearing tertiary branches. No. 57 (mut. *nitida*) was slightly taller than no. 28, almost simple, with leaves narrower than in the typical form, upwardly rolled parallel to the mid-vein, very glistening, nearly twice as thick as in normal

plants, and very brittle. A few seeds were obtained from this plant by self-pollination, but they did not germinate.

The 729 plants of Lexington C which were grown in 1913 yielded in all 6 different mutations. All of them except mut. *nitida* and mut. *nummularia* were infertile or nearly so to their own pollen. The latter type, in spite of the fact that it was unwittingly subjected to very unfavorable conditions, produced seeds from which a second generation has been grown. For fear of losing the 6 original plants, they were planted in the center bed of the greenhouse when the rest of the culture was transferred to the garden. Before it was realized how much their development was being retarded by the extreme heat in the greenhouse, it was too late to move them again with any prospect of success. Three plants died after they had begun to flower, but before any seeds were ripe.

The characters of mut. nummularia

A few plants of typical *O. pratincola* which were kept in the greenhouse with the mutation served to show that there are distinct differences in the habits of growth of the two types, when they are grown under identical conditions. This fact will be apparent from fig. 7, in which two sister plants of the same age are shown. It will be noticed that the stature of the mutation is less than that of the parent type, but that the lateral branches are more numerous and more densely leafy. A thoroughgoing comparison of the two types cannot be made until the cultures of 1914 shall have grown to maturity out of doors. The more striking contrasting characters, however, are the following:

In *O. pratincola*	In mut. *nummularia*
The early seedling leaves are ovate.	The early seedling leaves are orbicular.
The stem leaves are reflexed.	The stem leaves are involute.
The lower leaves of the lateral branches are ovate-lanceolate.	The lower leaves of the lateral branches are broadly ovate.
The ovary and calyx are sparsely pilose (sometimes almost glabrous).	The ovary and calyx are closely and finely pubescent.

In *O. pratincola*	In mut. *nummularia*
The hairs of the calyx segments and hypanthium are about 1 mm. long and all belong to the thick-walled, acute type with multicellular, tuberculate bases.	The hairs of the calyx segments and hypanthium are less than 0.5 mm. long and belong to two types: (1) acute, thick-walled hairs without multicellular, tuberculate bases, and (2) thin-walled, round-pointed clavate or cylindrical hairs.
The calyx segments separate in pairs.	The four calyx segments remain united when the flower opens.

The difference in the rupture of the calyx is shown in fig. 8. The writer is inclined to believe that the clear-cut qualitative distinction between the calyx pubescence of the parent form and that of the mutation will provide an absolute criterion for determining whether or not mut. *nummularia* marks an evolutionary advance over *O. pratincola*. A priori it seems to be a safe prediction that mut. *nummularia* will prove to be a progressive mutation of even more striking individuality than *O. gigas*.

It is unfortunate that data on reciprocal crosses between *O. pratincola* and mut. *nummularia* will not be available until next year. The first flowers of the original mutations were, of course, self-pollinated, and further work was prevented by the loss of the plants. This year (1914) the writer has numerous plants of mut. *nummularia* (primary mutations as well as F_1 plants) with which to make the necessary crosses.

The heritability of mut. nummularia

The three individuals of mut. *nummularia* which bore seeds were nos. 2, 17, and 21. Even these, however, wilted and dried up while still in flower, so that very few capsules were obtained. As in the case of many somewhat self-sterile Oenotheras, the capsules were small and contained few good seeds. From each of several capsules only one or two seeds were obtained, and the best had but 30, whereas a large capsule of typical *O. pratincola* contains well over 300. Until plants of the mutation shall have developed under more favorable conditions than those to which the first season's plants were subjected, it will be impossible to say

whether or not mut. *nummularia* is really as nearly self-sterile as this comparison would indicate. At any rate, only 403 seeds, many of them obviously too unripe to germinate, were obtained from 3 plants of the mutation. The seeds have given an F_1 progeny of 135 plants which is now (April 1914) in the early seedling stage.

The F_1 generation from mut. *nummularia* consists in part of plants which exactly reproduce the parental type and in part of secondary mutations. At the time this article is being written the plants are still young, but it is nevertheless clear (1) that the

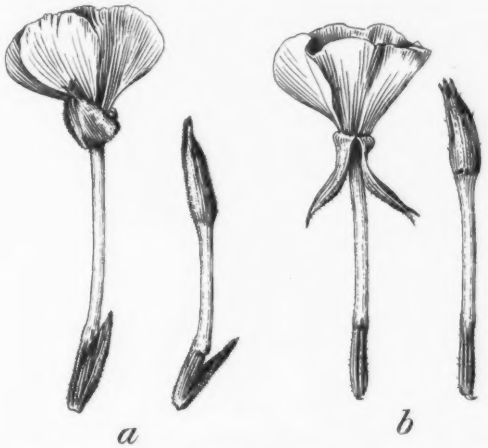

FIG. 8.—Flowers and buds of (*a*) *Oenothera pratincola* mut. *nummularia*, and (*b*) typical *O. pratincola*, showing especially the difference in the rupture of the calyx.

F_1 generation includes no typical *O. pratincola;* (2) that the secondary mutations (with one possible exception) are narrower leaved than *O. pratincola* and therefore even more sharply distinguished from mut. *nummularia* than the latter is from *O. pratincola;* and (3) that all of the secondary mutations (again with the single exception noted above) appear to be quite identical with certain primary mutations which have appeared simultaneously with mut. *nummularia* in various cultures of typical *O. pratincola*.

The secondary mutations fall into three well marked groups which have been called mut. *tortuosa*, mut. *rubricentra*, and mut.

subulata. It is of course impossible to establish absolute identities among seedling plants of types which have not yet been seen in flower. Consequently the F_1 progeny of mut. *nummularia* are classified either as true to type or as secondary mutations in table I, which shows the composition of the cultures now under observation.

TABLE I

COMPOSITION OF F_1 GENERATION OF MUT. *nummularia* (SEEDLING STAGE)

Parent	Number of seeds	Total plants	Mut. *nummularia*	Secondary mutations
Lex. C-2	15*	8	6	2
"	15*	6	5	1
"	30*	15	15	0
"	65	9	7	2
Lex. C-2 Total	125	38	33	5
Lex. C-17	39	14	12	2
Lex. C-17×C-21	20*	10	8	2
"	24*	2	2	0
"	11*	5	3	2
"	18*	5	5	0
"	64	25	15	10
Lex. C-17×C-21 Total	137	47	33	14
Lex. C-21	102	36	31	5
Grand total	403	135	109	26

*Indicates that the seeds were from one capsule.

Table I shows that only 34 per cent of the seeds of mut. *nummularia* germinated. In order to obtain as many plants as possible, a large number of seeds were counted into the seed pans which seemed too immature to germinate; 65 such seeds, planted by themselves, produced 9 plants. Part of the seeds planted were obtained from self-pollinated capsules, others from capsules which had been cross-pollinated. Table I shows that the progeny from the self-pollinated seeds includes secondary mutations and typical *nummularia* plants in the ratio 1:6. The same ratio for the progeny from cross-pollinated seeds is about 1:3.2. Although the difference in the ratio seems very marked, it may be due to the fact that the germination was poor and the cultures small.

Some of the progeny of two of the parents from which F_1 plants were obtained (Lexington C-17 and Lexington C-21) are shown in figs. 9–11. In fig. 9, no. 3 is a young specimen of mut. *tortuosa*, as yet only vaguely suggesting the characters which give this mutation its name. The other 5 plants are typical mut. *nummularia*, comparable in state of development with nos. 1 and 2 in fig. 3, and nos. 10 and 11 in figs. 5 and 6. Fig. 10 shows three of the types which are included in the F_1 cultures from mut. *nummularia*. Nos. 8 and 15 are characteristic plants of mut. *tortuosa;* nos. 13 and 16 are mut. *rubricentra;* nos. 35 and 36 are typical mut. *nummularia*. In order to show the striking uniformity of the *nummularia* plants 6 more of them are shown in fig. 11.

The frequency of mut. nummularia

In order to determine the frequency with which *O. pratincola* gives rise to mut. *nummularia*, large cultures were grown in the greenhouse during the winter of 1913–14. As usual, the seeds were sown on sterilized soil and transplanted to seed pans as soon after germination as circumstances permitted.[19] Remaining wild seeds of the original collections gave additional F_1 cultures of Lexington C, A, B, and E. F_1 cultures were also grown from the wild seeds of Lexington F, G, H, and I, which had not been previously planted. It will be remembered that mutations had been detected during the first year of cultivation only in Lexington C, and in this strain only because of the accidental application of the method of selective germination. The other strains were found to be quite as mutable as Lexington C when all of the seedlings were retained until old enough to show their distinctive characteristics. In addition to the F_1 cultures, F_2 cultures were grown from seeds of 8 self-pollinated F_1 sister plants of Lexington C, 1 self-pollinated plant of Lexington A, and 2 self-pollinated plants of Lexington B. These F_2 progenies from guarded seeds were found to contain approximately the same proportion of mutations as the F_1 progenies from unguarded wild seeds.

[19] The writer wishes to express here his appreciation of Mr. MARTIN BILON's painstaking and efficient care of the germination pans and the young seedlings.

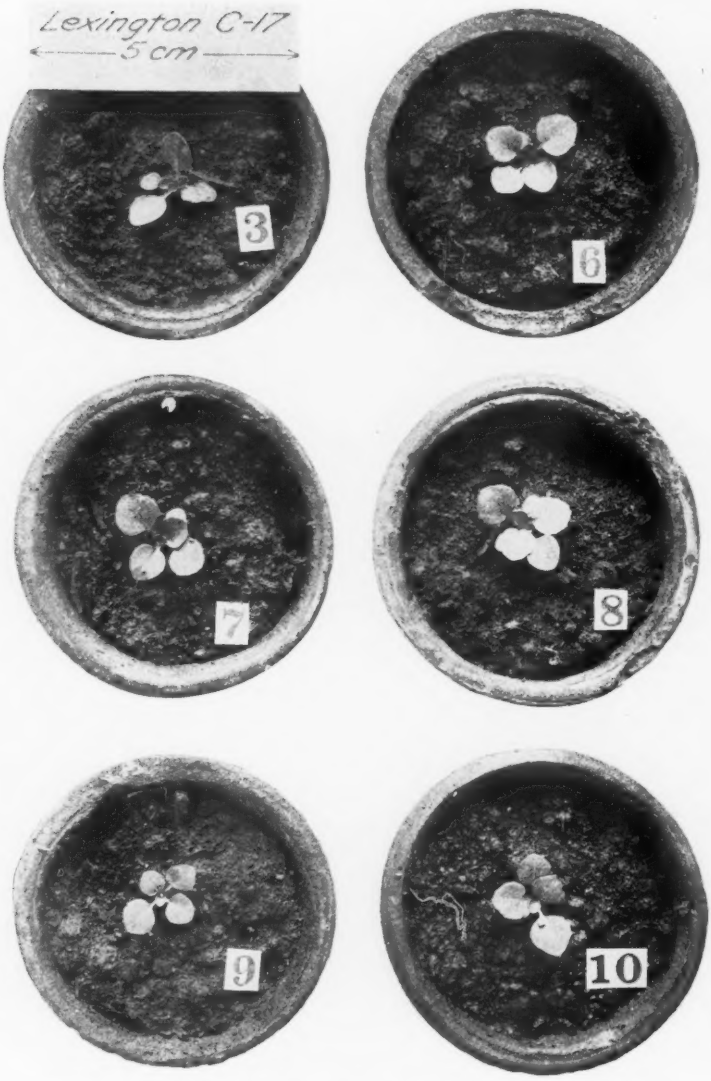

FIG. 9.—F_1 progeny of *Oenothera pratincola* mut. *nummularia*, Lexington C-17; the plant in the upper left-hand corner, Lexington C-17–3, is *O. pratincola* mut. *tortuosa*, here occurring as a secondary mutation, but seemingly the same as one of the very rarest primary mutations of *O. pratincola;* the other plants are typical examples of mut. *nummularia*.

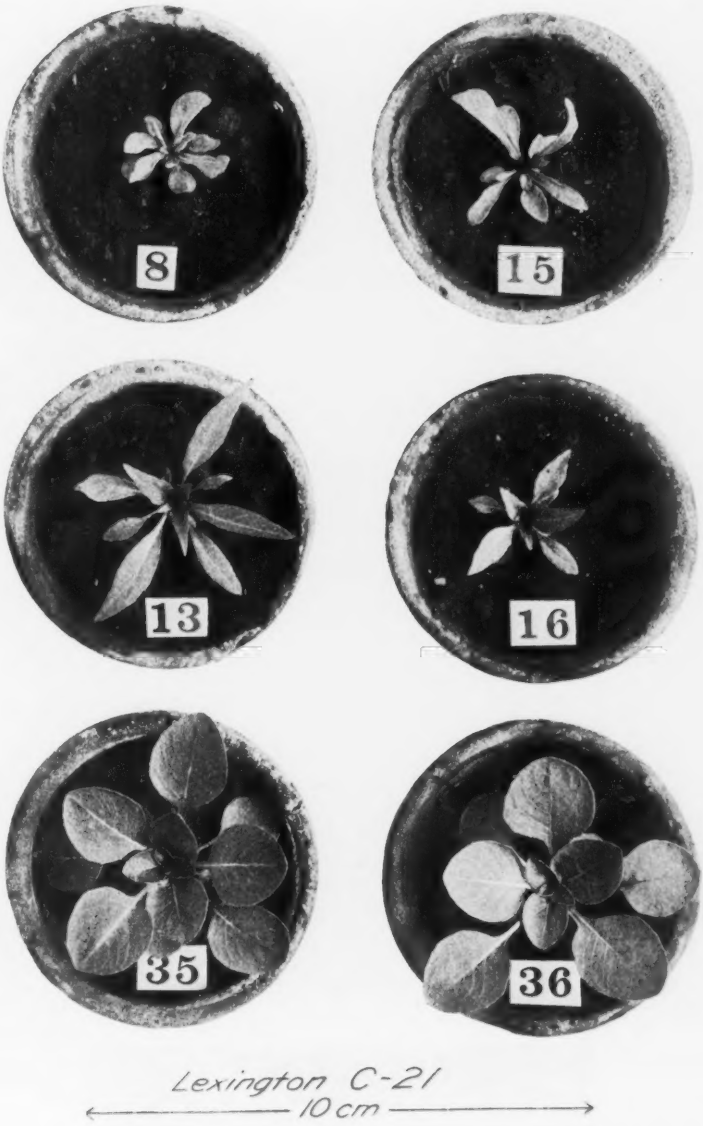

FIG. 10.—F_1 progeny of *Oenothera pratincola* mut. *nummularia*, Lexington C-21; the 2 upper plants, Lexington C-21–8 and C-21–15, are mut. *tortuosa;* the 2 in the middle row, C-21–13 and C-21–16, are mut. *rubricentra;* the 2 below are mut. *nummularia;* the plants shown in this cut are three weeks older than those shown in fig. 9.

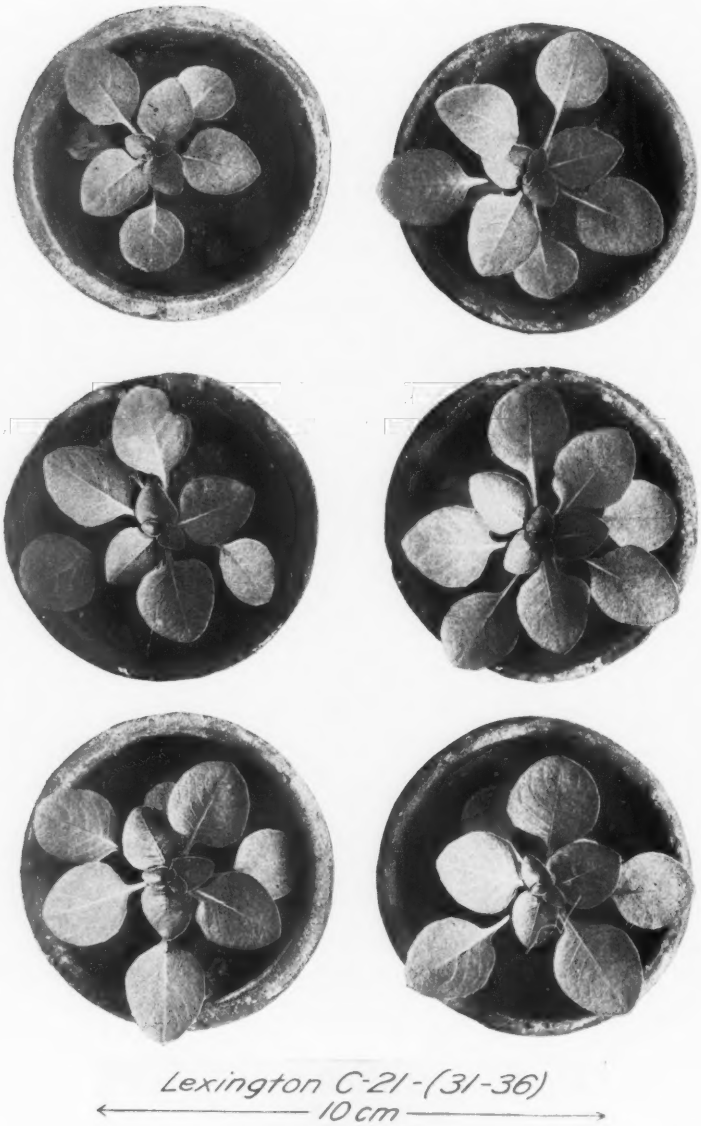

FIG. 11.—F_1 progeny of *Oenothera pratincola* mut. *nummularia;* typical examples of mut. *nummularia*, sister plants of those shown in fig. 10, of the same age.

Data in regard to the frequency of mut. *nummularia* in all the strains of *O. pratincola* except Lexington E are given in tables II–XI, and are summarized in table XII. Lexington E yielded striking mutations in both F_1 and F_2 generations, but they constituted an entirely different series of forms from those which were obtained from the other strains. In several respects the mutation phenomena presented by Lexington E were unique. It will be necessary, therefore, to defer an account of this strain until next year.

It will be noticed from the tables that a large number of seeds were planted capsule by capsule. The variation in number of seeds per capsule appears greater than it should, for in many cases the capsules had dehisced and lost part of their contents. In general, a capsule of *O. pratincola* contains 200–300 seeds.

TABLE II

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON C"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
2	1000	720	711	4 (nos. 10, 11, 17, and 21)	5
3	133*	104	93	0	8
4	130*	117	116	0	1
5	116*	111	106	0	5
6	88*	21	20	0	1
7	125*	20	20	0	0
8	162*	152	149	0	3
9	164*	143	140	0	3
10	237*	172	165	0	7
11	237*	223	211	1 (no. 123)	11
12	65*	35	35	0	0
13	217*	147	143	1 (no. 136)	3
14	200	156	153	0	3
15	200	154	152	0	2
16	147*	96	93	0	3
17	200	60	58	0	2
18	200	155	152	2 (nos. 150 and 151	1
19	200	98	95	0	3
20	200	130	124	2 (nos. 156 and 160)	4
21	200	112	109	1 (no. 162)	2
Total	4,221	2,923	2,845	11	67

* Indicates seeds from the same capsule.

TABLE III

ANALYSIS OF F_2 SEEDLING CULTURES OF "LEXINGTON C"

Parent	Culture	Number of seeds	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
Lex. C-5	1	244*	151	150	0	1
"	2	208*	155	154	0	1
"	3	190*	140	138	1 (no. 3)	1
Lex. C-5	Total	642	446	442	1	3
Lex. C-6	1	116*	41	39	0	2
"	2	106*	41	40	0	1
"	3	58*	31	27	0	4
"	4	41*	35	35	0	0
"	5	21*	10	10	0	0
"	6	14*	13	13	0	0
Lex. C-6	Total	356	171	164	0	7
Lex. C-15	1	196*	116	115	1 (no. 1)	0
"	2	233*	115	115	0	0
"	3	173*	106	106	0	0
"	4	134*	123	122	1 (no. 2)	0
"	5	28*	12	12	0	0
"	6	31*	12	12	0	0
"	7	48*	41	41	0	0
"	8	43*	32	31	1 (no. 11)	0
"	9	12*	9	9	0	0
"	10	17*	15	15	0	0
"	11	31*	15	15	0	0
Lex. C-15	Total	946	596	593	3	0
Lex. C-22	1	148*	122	119	0	3
"	2	203*	169	157	1 (no. 9)	11
"	3	172*	147	142	1 (no. 20)	4
"	4	225*	189	184	1 (no. 21)	4
"	5	250*	196	191	0	5
Lex. C-22	Total	998	823	793	3	27
Lex. C-36	1	182*	142	141	0	1
"	2	208*	150	147	0	3
"	3	210*	159	157	0	2
"	4	231	181	179	0	2
"	5	147*	99	96	0	3
Lex. C-36	Total	978	731	720	0	11
Lex. C-52	1	215*	148	146	1 (no. 1)	1
"	2	118*	100	100	0	0
"	2	189*	138	136	0	2
"	4	150*	75	73	1 (no. 28)	1
"	5	225*	173	173	0	0
Lex. C-52	Total	897	634	628	2	4

TABLE III—*Continued*

Parent	Culture	Number of seeds	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
Lex. C-72	1	192*	171	165	1 (no. 6)	5
"	2	223*	180	179	0	1
"	3	235*	187	186	0	1
"	4	279*	242	241	0	1
"	5	280*	230	225	0	5
Lex. C-72	Total	1,209	1,010	996	1	13
Lex. C-91	1	185*	146	144	2 (nos. 1 and 2)	0
"	2	284*	245	243	1 (no. 4)	1
"	3	245*	172	171	0	1
"	4	267*	125	121	0	4
"	5	316*	198	195	0	3
"	6	337*	300	293	5 (nos. 39, 40, 42, 43, 44)	2
"	7	242*	187	181	0	6
Lex. C-91	Total	1,876	1,373	1,348	8	17
Eight F_1 plants	Grand total	7,902	5,784	5,684	18	82

* Indicates seeds from the same capsule.

TABLE IV

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON A"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
2	341*	66	59	0	7
3	405*	129	118	2 (nos. 44 and 45)	9
4	337*	60	53	2 (nos. 53 and 54)	5
Total	1,083	255	230	4	21

* Indicates seeds from the same capsule.

TABLE V

ANALYSIS OF F_2 SEEDLING CULTURES OF "LEXINGTON A"

Parent	Culture	Number of seeds	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
Lex. A-5	1	119*	76	73	0	3
"	2	200	115	110	0	5
"	3	200	118	115	2 (nos. 9 and 11)	1
"	4	200	127	122	1 (no. 15)	4
Lex. A-5	Total	719	336	420	3	13

* Indicates seeds from the same capsule.

TABLE VI

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON B"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
2	149*	107	95	0	12
3	324*	188	175	0	13
4	247*	107	97	0	10
5	200*	106	101	0	5
Total	920	508	468	0	40†

* Indicates seeds from the same capsule.

† Of the 40 mutations and suspected mutations, 36 were merely smaller plants than the average, selected in the expectation that some might prove to be dwarfs.

TABLE VII

ANALYSIS OF F_2 SEEDLING CULTURES OF "LEXINGTON B"

Parent	Culture	Number of seeds	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
Lex. B-1	1	184*	157	157	0	0
"	2	269*	142	137	0	5
"	3	264	221	215	1 (no. 8)	5
"	4	195*	154	152	1 (no. 12)	1
Lex. B-1	Total	912	674	661	2	11
Lex. B-2	1	106*	72	68	0	4
"	2	250*	147	142	2 (nos. 26, 27)	3
"	3	284*	176	171	0	5
"	4	111*	82	80	0	2
"	5	113*	94	92	0	2
Lex. B-2	Total	864	571	553	2	16
Two F_1 plants	Grand total	1,776	1,245	1,214	4	27

* Indicates seeds from the same capsule.

TABLE VIII

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON F"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
1	92* (large, immature)	68	62	1 (no. 1)	5
2	139* (mature)	34	31	0	3
Total	231	102	93	1	8

* Indicates seeds from the same capsule.

TABLE IX

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON G"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
1	87* (very large, immature)	25	25	0	0
2	50* (large, immature)	17	17	0	0
3	285*	157	152	0	5
4	160	140	139	0	1
5	159*	136	133	2 (nos. 47, 49)	1
6	152*	95	93	0	2
7	187*	153	152	0	1
8	144*	86	80	0	6
9	120*	106	99	0	7
10	197*	157	154	1 (no. 54)	2
11	133*	98	97	0	1
12	147*	114	110	1 (no. 52)	3
Total	1,821	1,284	1,251	4	29

* Indicates seeds from the same capsule.

TABLE X

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON H"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
1	301*	152	145	2 (nos. 3 and 4)	5
2	157*	78	76	0	2
Total	458	230	221	2	7

* Indicates seeds from the same capsule.

TABLE XI

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON I"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
1	125*	57	53	0	4
2	206*	147	145	1 (no. 13)	1
3	244* (immature)	64	61	2 (nos. 14 and 15)	1
Total	635	268	259	3	6

* Indicates seeds from the same capsule.

TABLE XII

SUMMARY OF TABLES II–XI, SHOWING THE FREQUENCY WITH WHICH *O. pratincola* GIVES RISE TO MUT. *nummularia*

Strain	Generation	Number of seeds	Number of plants	Germination per cent	Number of mut. *nummularia*	Ratio of mut. *nummularia* to seeds planted	Ratio of mut. *nummularia* to total plants
Lex. A ..	F_1	1083	255	23.5	4	1:271	1:64
" ..	F_2	719	436	60.6	3	1:240	1:145
Lex. A ..	F_1 & F_2	1,802	691	38.4	7	1:257	1:99
Lex. B ..	F_1	920	508	55.2	0		
" ..	F_2	1776	1245	70.1	4	1:444	1:311
Lex. B ..	F_1 & F_2	2,696	1,753	65.0	4	1:674	1:438
Lex. C ..	F_1	4221	2923	69.3	11	1:384	1:266
" ..	F_2	7902	5784	73.2	18	1:439	1:321
Lex. C ..	F_1 & F_2	12,123	8,707	71.8	29	1:418	1:300
Lex. F ..	F_1	231	102	44.2	1	1:231	1:102
Lex. G ..	F_1	1,821	1,284	70.5	4	1:455	1:321
Lex. H ..	F_1	458	230	50.2	2	1:226	1:115
Lex. I...	F_1	635	268	42.2	3	1:212	1:89
All.....	F_1	9,369	5,570	59.5	25	1:375	1:223
"	F_2	10,397	7,465	71.8	25	1:416	1:299
All.....	F_1 & F_2	19,766	13,035	66.0	50	1:395	1:261

In all, there were 19,766 seeds sown of the 7 strains which gave rise to mut. *nummularia*. They gave 13,035 seedlings, of which 5,570 belonged to F_1 and 7,465 to F_2 progenies. The average germination of the F_1 seeds was 59.5 per cent, or 58 per cent if the 1000 seeds of Lexington C sown in the winter of 1912–1913 are not figured in. Most of the F_1 seeds were over a year old when they were planted. The germination of the F_2 seeds, which were sown soon after they were harvested, was 71.8 per cent. Inspection of table XII shows the remarkable fact that the ratio of mut. *nummularia* to seeds planted was nearly identical for the F_1 and F_2 progenies, 1:375 in the one case, 1:416 in the other, but that the

ratio of *nummularia* mutations to plants showed a variation roughly commensurate with the difference in germinability between the F_1 and F_2 seeds. In other words, the mortality among the year-old F_1 seeds appears to have been largely confined to seeds of typical *O. pratincola*. The ratio of *nummularia* mutations to seeds planted is seen from table XII to be reasonably constant for all 7 strains in both the F_1 and F_2 generations. The ratio of mutations to total plants, however, varies between wide limits, and in every case a low percentage of germination is associated with a high frequency of mutation. The F_1 progeny of Lexington A, for example, included 4 individuals of mut. *nummularia* among 255 plants, a ratio of 1:64. These 255 plants, however, were obtained by sowing 1,083 seeds, of which only a small proportion (23.5 per cent) germinated. There seems no escape from the conclusion that the percentage of germinable seeds of mut. *nummularia* had increased by virtue of the greater mortality among the seeds of typical *O. pratincola*.

The evolutionary significance of differential mortality is too obvious to require any lengthy discussion. Mut. *nummularia* has a distinctly greater survival value than its parent when subjected to conditions which delay germination. It has already been shown that mut. *nummularia* has an enormously greater chance to survive than typical *O. pratincola* when subjected to certain unfavorable soil conditions. These facts should be carefully weighed by critics of the mutation theory who persist in assuming, as a matter of course, that mutations would have no chance to survive in competition with the more numerous typical plants. DE VRIES[20] has already shown that the percentage of mutation in a culture of *O. Lamarckiana* from seeds 5 years old was 40 per cent instead of the usual 6 per cent. In his comment on this remarkable result he states that in general the seeds of the mutation remain germinable longer than those of typical *O. Lamarckiana*, and suggests that it might be possible to make use of differential mortality to increase the proportion of mutations in seeds, and thereby to facilitate the discovery of the mutations. The writer unconsciously put this suggestion to a test at the time mutations

[20] DE VRIES, H., Die Mutationstheorie 1:186. 1901.

were first found in *O. pratincola*. HUNGER[21] has recently recorded observations on selective mortality in the seeds of *O. Lamarckiana* which can only be interpreted as showing that the mutations of this species have decidedly a greater survival value than the parent form.

It is often remarked that the Onagras are not most usually found in undisturbed habitats with other native plants, but rather as weeds in fields and waste places, among the aliens of our flora. Wherever the soil is disturbed, as by plowing, road-making, excavating, they are frequently found in large numbers. They often dominate the flora on made land and on new railroad embankments, but are for the most part replaced by other weeds when the soil ceases to be disturbed at intervals. A fallow field which contains many Onagras for a season or two after cultivation is discontinued will thereafter contain fewer each year. If again plowed, it will apparently be restocked by the germination of seeds which have lain dormant, perhaps for years. Selective mortality among dormant seeds might result in such a field being restocked with plants among which mutations would be unexpectedly numerous.

The most interesting fact shown by table XII is that the frequency of mut. *nummularia* cannot correspond with any Mendelian ratio except that of a tetrahybrid splitting in the ratio 255:1. In the case of a number of progenies, to be sure, the ratio of mutations to plants more nearly approximates the trihybrid ratio 63:1, but it has already been shown that in each such instance the high mutation ratio is associated with a low percentage of germination. When the ratio of mutations to seeds is dealt with, there is no case of an approximation to the 63:1 ratio. The data of table XII, recalculated, are stated in table XIII in such form as to show that no single progeny was large enough to prove that the 255:1 ratio might not be the true one. On the contrary, the data afford no reason to believe that the mutation ratio is 255:1. It may be because of the smallness of the cultures that no single progeny shows a significant deviation from this ratio.

[21] HUNGER, F. W. T., Recherches expérimentales sur la mutation chez *Oenothera Lamarckiana*, executées sous les tropiques. Ann. Jard. Buitenzorg **27**:92–113. 1913.

Turning again to table XII, it is seen that the progenies might possibly be assembled in two groups, those with a mutation ratio of approximately 400:1 (group I of table XIII), and those with a ratio of about 250:1 (group II of table XIII). Testing separately the ratios from these groups (see table XIII), we find that the number of individuals in group II is too small to establish a significant deviation from the ratio for group I. (The difference is 0.18 ± 0.13 per cent). It is therefore impossible to demonstrate either that the mutation ratio is or that it is not the same for all the progenies.

TABLE XIII

TEST OF THE FITNESS OF THE MUTATION RATIOS TO THE NEAREST MENDELIAN RATIO (235:1)

Culture	Group	Class 0 per cent not mut. *nummularia*	Class 1 per cent mut. *nummularia*	Number of seeds planted (n.)	Standard deviation ($\sigma = \sqrt{\%p_0 \cdot \%p_1}$)	Mean error in per cent ($m = \frac{\sigma}{\sqrt{n}}$)	Expectation for each value of n if ratio is 255:1	Difference between observation and expectation
Lex. A-F_1	II	99.63	0.37	1,083	6.07	0.18	0.39 ± 0.19	0.02 ± 0.26
Lex. A-F_2	II	99.58	0.42	719	6.47	0.24	0.39 ± 0.24	0.03 ± 0.34
Lex. B-F_2	I	99.77	0.23	1,776	4.79	0.11	0.39 ± 0.15	0.16 ± 0.29
Lex. C-F_1	I	99.74	0.26	4,221	5.10	0.08	0.39 ± 0.10	0.13 ± 0.13
Lex. C-F_2	I	99.77	0.23	7,902	4.79	0.05	0.39 ± 0.07	0.16 ± 0.09
Lex. F-F_1	II	99.57	0.43	231	5.42	0.42	0.39 ± 0.41	0.04 ± 0.59
Lex. G-F_1	I	99.78	0.22	1,821	4.68	0.11	0.39 ± 0.15	0.17 ± 0.29
Lex. H-F_1	II	99.56	0.44	458	6.59	0.31	0.39 ± 0.29	0.05 ± 0.43
Lex. I-F_1	II	99.53	0.47	635	6.86	0.36	0.39 ± 0.25	0.08 ± 0.44
Group I		99.76	0.24	15,720	4.89	0.04	0.39 ± 0.05	0.15 ± 0.06
Group II		99.58	0.42	3,126	6.47	0.12	0.39 ± 0.11	0.03 ± 0.16
Groups I & II		99.75	0.25	18,846	5.00	0.04	0.39 ± 0.05	0.14 ± 0.06
Total		99.75	0.25	19,766	5.00	0.04	0.39 ± 0.04	0.14 ± 0.06

If we assume that it is justifiable to treat all of the progenies as one group, the numbers are then large enough to indicate, not however without considerable doubt, that the frequency of occurrence of mut. *nummularia* is not in accord with the tetrahybrid ratio 255:1, but with some ratio lying between 330:1 and 450:1. Of course we cannot assume that there is no mortality at all among the seeds which produce mut. *nummularia*. If in the 30 per cent of seeds *O. pratincola* which never germinate even when fresh the mortality among mutations and non-mutations were the same, then the mutation ratio would not significantly deviate from 255:1. It

is obvious that a Mendelian explanation of the occurrence and frequency of mut. *nummularia* involves the assumption that each parent plant which gave rise to it was heterozygous with regard to at least four factors. Otherwise no segregate would occur with so low a frequency as 1:255. The following objections to a Mendelian explanation may be enumerated:

1. *O. pratincola* is probably almost invariably self-pollinated in a state of nature, for the anthers burst in contact with the receptive stigma the day before the flowers open. In a very few generations heterozygosis would be eliminated from a strain which had accidentally become crossed. Hybridization involving four factors, followed by several generations of self-pollination, would result in an F_2 with 6.25 per cent of homozygotes, an F_3 with 31.64 per cent, F_4 with 58.62 per cent, F_5 with 93.75 per cent, F_6 with 96.87 per cent, F_7 with 98.44 per cent, F_8 with 99.22 per cent, F_9 with 99.61 per cent, F_{10} with 99.80 per cent, etc. It would be utterly absurd to suggest that out of 8 wild mother plants growing far apart, selected at random, 7 were tetrahybrids.

2. An F_1 tetrahybrid would invariably show segregation in a 255:1 ratio. Out of its F_2 progeny, however, only one plant in 16 would be a tetrahybrid, and therefore only one F_2 plant in 16 could exhibit 255:1 segregation in the F_3. The other F_2 heterozygotes would be hybrids of a lower order. Some would segregate in the ratio 63:1, some in the ratio 15:1, and some in the ratio 3:1. It has already been pointed out (see tables III, V, and VII, summarized in tables XII and XIII) that every F_1 (that is, F_1 with regard to the wild mother plants from Lexington) plant of which seeds were planted either yielded a progeny containing no *nummularia* mutations, in which case the number was not large enough to be sure of getting this mutation, or else the only Mendelian ratio indicated as possible was 255:1. In all, 11 F_2 progenies were grown, of which only 2 failed to give the mutation. The only uncomplicated Mendelian explanation requires that in picking 11 mother plants at random from among 142 F_1 plants, 9 were selected from that one-sixteenth of the culture which was still heterozygous for four characters. It may be pointed out that among 142 plants, just 9 tetrahybrids might reasonably be expected. The chances

are infinitesimal that all 9 would be included among 11 plants chosen at random.

3. A tetrahybrid might give as many as 16 phaenotypes in the F_2. All of these would have a greater frequency than 1:255 except the pure recessive. We have seen that mut. *nummularia* cannot have a greater frequency than 1:255, and have also seen that it is not a pure recessive, for in the next generation after it originates it gives rise to several distinct types.

4. In the case of one F_2 progeny (Lexington C-91, see table III) from a single mother plant, 1,539 seeds from 6 capsules gave 3 specimens of mut. *nummularia*, whereas 337 seeds from one capsule gave 5. Such a result shows a frequency varying from 1:60 to 1:513 on capsules from the same spike. From a Mendelian standpoint it is practically impossible to explain such a result.

The mutation phenomenon in *O. pratincola* cannot be explained away by any reasonably plausible stretching of Mendelian theory. On the contrary, it seems obvious that mutation is quite a different process from hybrid segregation, although both processes may occur simultaneously.

Mut. *nummularia* is the only one of the mutations of *O. pratincola* the frequency of which has been determined. None of the others has been observed throughout the complete cycle from seed to seed and carried into a second generation. In tables II–XI all of the variants except mut. *nummularia* are thrown together as "other mutations or suspected mutations." In explanation of this mixed category, it is necessary to state that all unusually small or unusually large plants, regardless of whether or not they appeared otherwise different from the mass of the culture, were counted as "suspected mutations," in order to be sure that no such variation as a mut. *nanella* would be passed over. To judge from past experience, most of the "suspected mutations" will develop as quite normal plants. Consequently the mutability of *O. pratincola* is probably not as great as might be assumed from the tables.

Mut. Mummularia a discontinuous variation

Critics of DE VRIES' work on mutation in *Oenothera Lamarckiana* have not infrequently expressed skepticism as to whether or not the

mutations were actually unconnected with the parent form by intermediates, which might have been overlooked in classifying the young seedlings. An endeavor has been made to forestall the same criticism of the writer's work on *O. pratincola* by the publication

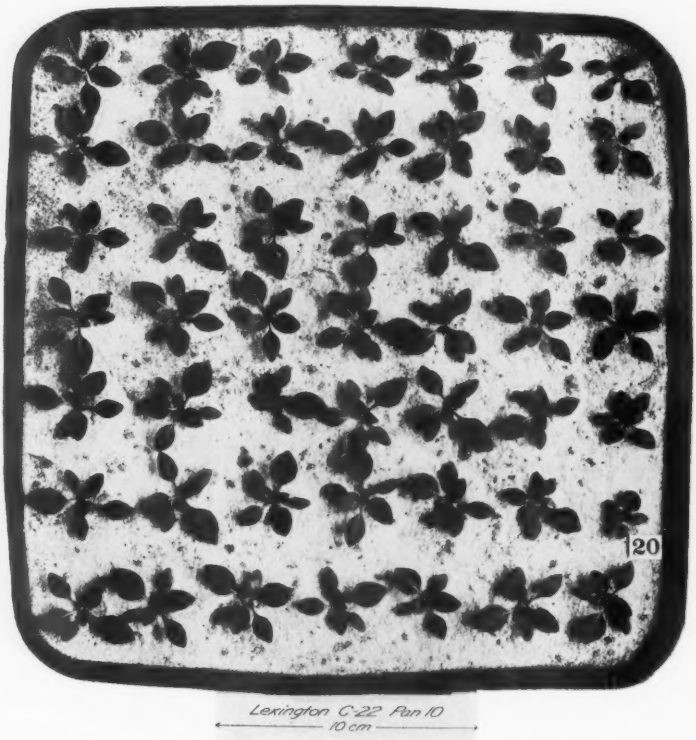

FIG. 12.—F_2 progeny of Lexington C, *Oenothera pratincola* (pan 10 of the progeny of C-22); the only mutation shown is C-22–20, mut. *nummularia;* the other plants are typical *O. pratincola*.

of a series of photographs showing some of the pans in which the mutations occurred. Each reader can judge for himself as to the discontinuity of the mutations from the rest of the plants. It is believed that no one has heretofore published so extensive a series of photographs representing random samples of cultures from which

none of the seedlings had been discarded. It must be remembered that each pan is a fair sample of a whole culture, for the seedlings were pricked off when very small and were taken from the seed pan as they came, with no attempt at sorting.

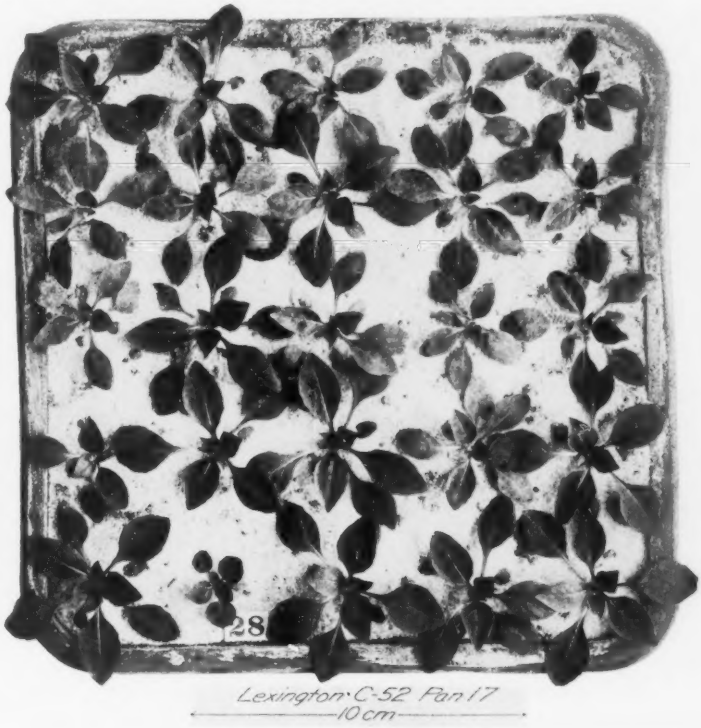

FIG. 13.—F_3 progeny of Lexington C, *Oenothera pratincola* (pan 17 of the progeny of C-52); one example of mut. *nummularia*, C-52-28, is shown; the remaining plants are typical.

Figs. 5, 6, 12, 13, 14, 15, and 17 show 7 of the 50 occurrences of mut. *nummularia* in cultures aggregating 13,035 plants. Three more of the original plants of this mutation are shown in figs. 3, 4, and 16. The figures showing entire pans should give a fairly clear idea of what the writer interpreted as fluctuating variation. It is believed that very few if any mutations escaped detection in the

cultures of 1914. The two mutations of Lexington C (nos. 28 and 57) which passed muster as typical plants when the seedlings of 1913 were examined would probably not have been missed in the

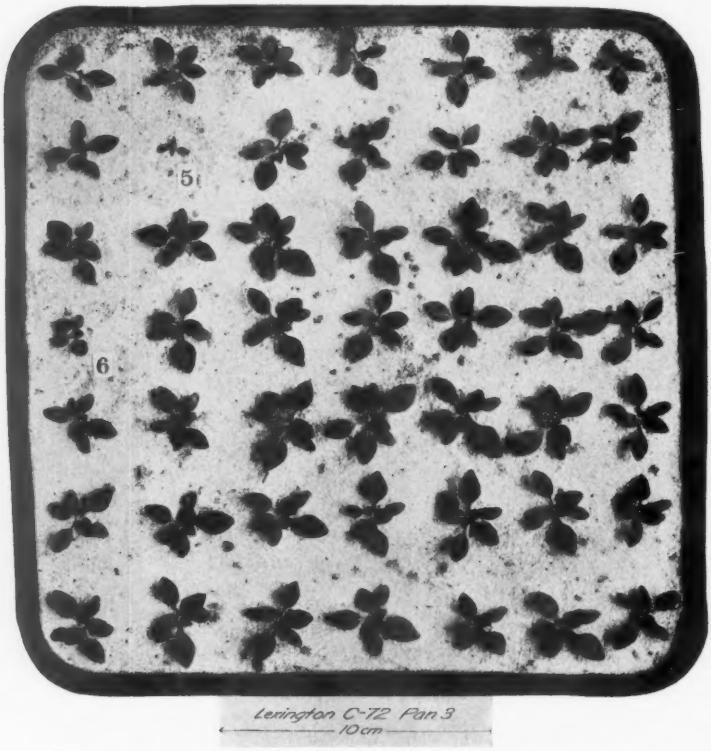

FIG. 14.—F_2 progeny of Lexington C, *Oenothera pratincola* (pan 3 of the progeny of C-72); two mutations are shown, mut. *subulata*, C-72–5, and mut. *nummularia*, C-72–6; the other plants are typical.

more searching scrutiny which the seedlings of 1914 underwent.[22] Although some of the mutations cannot be distinguished in the young seedling stage with ease, it is believed that the likelihood

[22] Mut. *nitida*, represented by Lexington C-57 in the cultures of 1913, occurred several times in 1914 and was detected in the young seedling stage in every case Nov. (1914).

of mistaking mut. *nummularia* for the parent type or for one of the other mutations is negligible. The orbicular seedling leaves are too striking a characteristic to be overlooked.

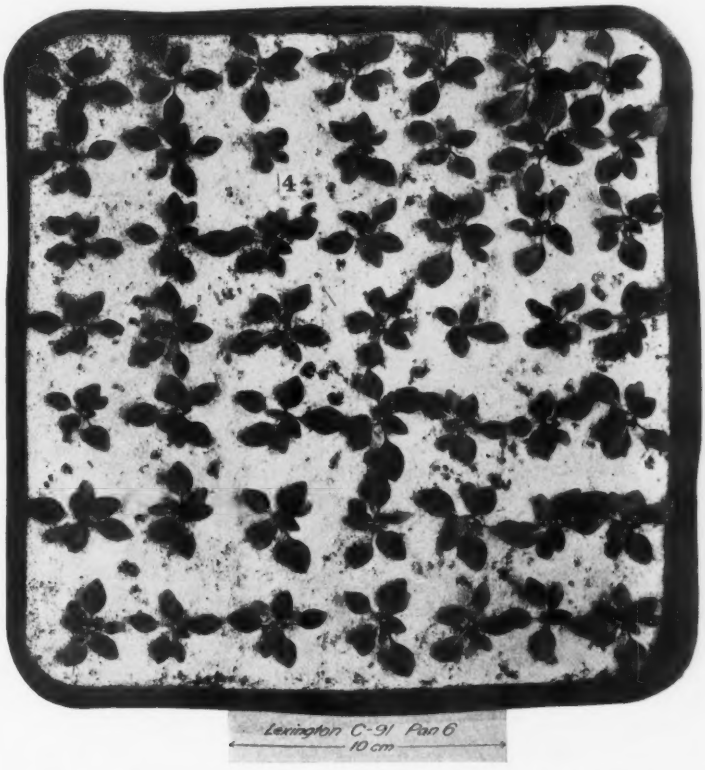

FIG. 15.—F_2 progeny of Lexington C, *Oenothera pratincola* (pan 6 of the progeny of C-91); one plant of mut. *nummularia* is shown, C-91–4; the other plants are typical.

The unlikeness of mut. nummularia and O. pratincola × O. numismatica

Before mut. *nummularia* had been found in F_2 progenies from guarded seed, it seemed possible that it might be an F_1 hybrid of *O. pratincola* with some other wild species, of which a few pollen

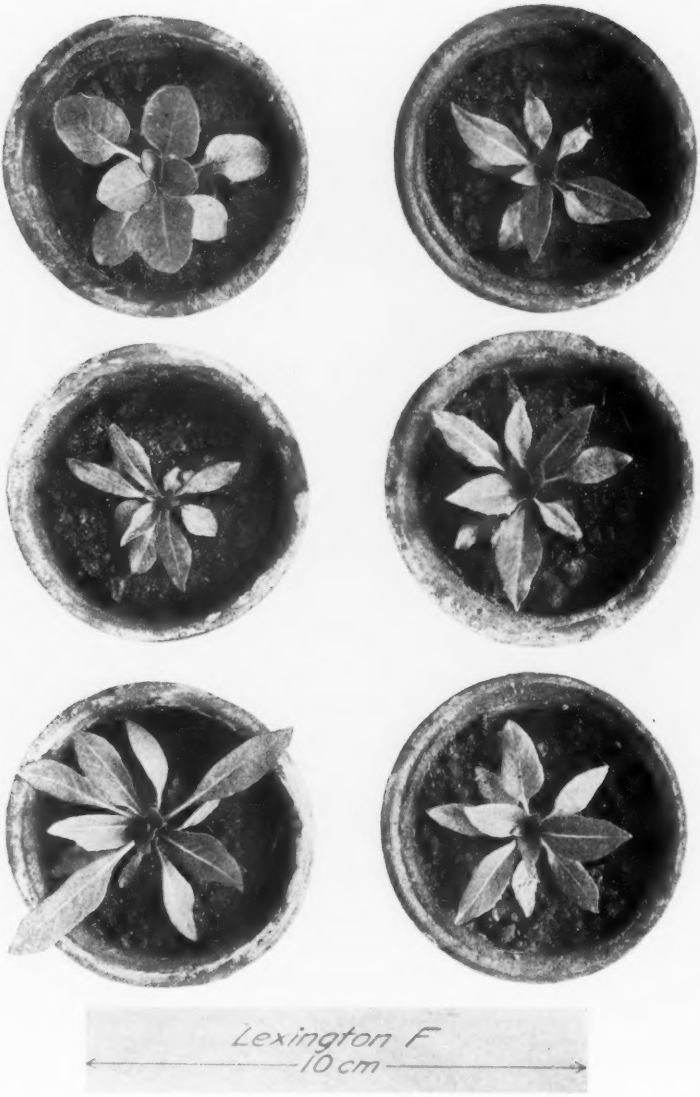

FIG. 16.—Mutations from the F_1 progeny of Lexington F, *Oenothera pratincola;* the plants are F-1, mut. *nummularia;* F-2, -4, -5, -6, mut. *rubricentra;* F-3, mut. *tortuosa* (?), taking the plants in order from the upper left-hand corner.

grains had accidentally reached the stigmas of the mother plants. This hypothesis was tested by crossing *O. pratincola* with *O. numismatica*. As already stated, these two species were the only Onagras which the writer found at Lexington. The latter, furthermore, is

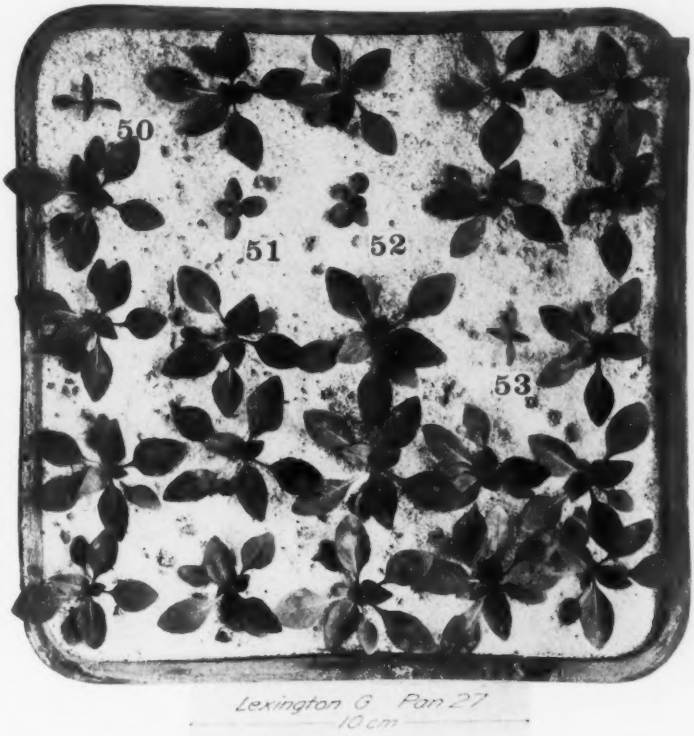

FIG. 17.—F_1 progeny of Lexington G, pan 27, *Oenothera pratincola;* four mutations are shown, G-50 and G-53, mut. *rubricentra;* G-51, mut. *nitida;* G-52, mut. *nummularia;* the other plants are typical *O. pratincola*.

suspiciously similar in several characters to mut. *nummularia*, as may be seen by comparing the characters already recorded. The cross *O. pratincola* ♀ × *O. numismatica* ♂ was conspicuously fertile; 326 seeds from one capsule gave a culture of 222 plants, consisting

of twin hybrids and one mutation. The solitary exception was broader leaved than the rest of the culture and is interpreted by the writer as the product of a cross between a mutated ♀ gamete, which if pollinated by *O. pratincola* would have yielded mut. *nummularia*, and a normal ♂ gamete of *O. numismatica*. This hypothesis will be tested later by appropriate crosses. It is clear that a cross between *O. pratincola* and *O numismatica* does not yield mut. *nummularia*, or anything resembling it, with greater frequency than does unhybridized *O. pratincola*. Perhaps *O. numismatica* is itself a mutation from *O. pratincola*, or a form which has segregated from the cross mut. *nummularia* × *O. pratincola*. One would expect the latter cross to occur rather often if, as seems to be the case, mut. *nummularia* itself is partially self-sterile. It seems not unlikely that in nature self-sterile or nearly self-sterile mutations may be perpetuated by effective cross-pollination, either as stable hybrids or as homozygous forms resulting from subsequent segregation. It is an interesting fact that although *O. pratincola* has a very high proportion of good pollen grains (90 per cent or more), mut. *nummularia* rarely has pollen which is 50 per cent perfect, and some anthers produce no good pollen at all.

Conclusions

1. *Oenothera pratincola*, a recently described small-flowered self-pollinating species from Kentucky, is in a mutating condition comparable with that of *O. Lamarckiana*.

2. The most striking of the mutations, *O. pratincola* mut. *nummularia*, occurred in strains derived from 7 wild mother plants out of 8 selected at random.

3. In two of these strains the mutation was found in both the F_1 and F_2 generations from the parent plant. In a third strain the mutation was found only in the F_2 generation, but a sufficient number of F_1 plants had not been grown to insure its detection in that generation.

4. Mut. *nummularia* appears to occur with a frequency of about one individual to each 300–400 seeds planted. The several progenies showed no significant variation in the mutation ratio.

5. The mutation ratio cannot be explained on Mendelian grounds.

6. Mut. *nummularia* is better adapted than the parent type to withstand influences unfavorable to germination. In every case where a progeny contained an unexpectedly large number of mutations, the germination was correspondingly poor.

7. Selective germination and differential mortality among dormant seeds may be important factors in natural selection.

8. Mutation is a distinct process from Mendelian segregation, and the phenomena exhibited by *Oenothera Lamarckiana*, *O. biennis*, and *O. pratincola* cannot be attributed to heterozygosis.

Bureau of Plant Industry
Washington, D.C.

THE EMBRYO SAC AND EMBRYO OF STRIGA LUTEA

MARGARET R. MICHELL

(WITH PLATES VIII AND IX)

Attention lately has been drawn to *Striga lutea*, a semi-parasitic plant belonging to the Rhinanthoideae-Gerardieae (8) group of the Scrophulariaceae, owing to the ravages caused by it in the maize crops in parts of South Africa.

The material for this investigation was obtained by Dr. H. H. W. PEARSON in Pretoria during the autumn of the years 1912 and 1913.

The ovaries were fixed in a chromacetic solution and the chief stain used was Haidenhain's iron-hematoxylin. A combination of diamant fuchsin and light green also gave good results, and Flemming's triple stain gave excellent differentiation in the embryonic stages.

Ovule and embryo sac

There is nothing striking in the ovary. It is of the ordinary bilocular scrophulariaceous type, and bears a large number of minute anatropous ovules on the rather swollen placentae. Many of the ovules possess long funicles, and in some cases the funicle branches and bears two ovules. The fact that the length of funicle varies enables the plant to produce a greater number of ovules per unit area of placenta than it would be able to do were the funicles all of one length.

The archesporium can be distinguished at an early stage before the integument arises. It consists of a single hypodermal cell which, without undergoing division, becomes directly the megaspore mother cell. This is shown in fig. 1, which also shows the origin of the integument. The young ovule grows with great rapidity, and before the first division of the nucleus of the megaspore mother cell, the integument is well marked and the whole ovule is rapidly assuming its mature anatropous form.

The nucellus consists of one layer of cells. As development proceeds the cells become flattened and finally disorganized, so that

when the embryo sac has reached maturity, only traces of it are to be found lying between the integument and the embryo sac.

The bulk of the ovule is composed of the thick integument, as is often the case in the Scrophulariaceae. Fig. 2 represents a transverse section through the ovule just above the integument and shows the nucleus of the mother cell in synapsis, prior to its first division. In the ovule drawn the nucleolus is just visible, but in many similar ovules it has disappeared. It was observed that, when synapsis occurs, about 10 per cent of the ovules in an ovary are in this stage simultaneously. Other stages in the heterotypic division were not seen, the next stage being that of the homotypic division (fig. 3). Fig. 4 shows the three upper megaspores degenerating, while the fourth has become the embryo sac.

The development of the embryo sac is perfectly normal. The nucleus divides and the resulting nuclei pass one to each pole of the embryo sac, the center being occupied by a large vacuole (fig. 5). These nuclei divide twice (figs. 6–8), thus giving two groups of four nuclei, one at each end of the sac. One nucleus from each group then moves toward the center (fig. 9); these two nuclei meet and fuse in the upper part of the sac, not far from the egg cell (fig. 10). BALICKA-IWANOSKA (1) found in certain genera of the Scrophulariaceae that the polar nuclei fuse about the middle of the embryo sac and migrate toward the egg at the time of fertilization. SCHMID (13) pointed out that this position of the polar nuclei at the time of fusion is not that always found in this family. He found that the position at the time of fusion may vary in a single species. For instance, in *Pedicularis palustris* the polar nuclei may fuse in the upper, lower, or middle part of the sac. In the cases in which fusion occurs in the middle or at the base of the sac, they migrate toward the egg at the time of fertilization.

The synergids have assumed a caplike appearance by the time the embryo sac is ready for fertilization. In the embryo sac shown in fig. 11 this cap is not yet developed, but the synergids are early distinguished from the egg by their much smaller size. In this figure the antipodals show signs of disintegration, and at the stage represented in fig. 12 a small deeply staining mass is all that is left of them.

In general behavior this embryo sac differs in no way from the rest of the Scrophulariaceae, in which it is a general rule that the synergids are well marked off from the other nuclei of the embryo sac, and the antipodals are inconspicuous, disappearing about the time of maturity.

Case of an ovule with two embryo sacs

In an ovary in which most of the ovules were in the 4-nucleate or 8-nucleate stages, one ovule was seen showing two sacs lying side by side. Fig. 18 represents a section through this ovule not passing through the embryo sacs. In this section the ovule has every appearance of having been derived from two fused ovules. Figs. 16 and 17 support this view, as the cells separating the two embryo sacs clearly belong to the integument. Unfortunately the sections through this ovule are oblique. Figs. 13–17 are drawn from this ovule as it was represented in five consecutive sections. The left-hand embryo sac has four nuclei arranged in two groups of two each. The right-hand embryo sac contains eight nuclei apparently not definitely arranged in groups. Six of the nuclei lie fairly close together at one end of the sac and two at the other end. Possibly this lack of arrangement is to be correlated with the abnormal conditions under which the sac has developed. This ovule was the only one showing any abnormal tendencies.

Cases in which two ovules have grown together to form one with two embryo sacs have not been reported as frequently as those in which the two embryo sacs arise from a single archesporium. They have been recorded, however, in *Pirus Malus*, *Loranthus europaeus*, and *Viscum album* (**5**).

Fertilization

Ovules in which fertilization is taking place are fairly abundant. In the section represented in fig. 12 the pollen tube is seen having penetrated the embryo sac and apparently pushed its way through one of the synergids, and has discharged its contents into the sac. One male nucleus is seen fusing with the egg, while the other is fusing with the nucleus produced by the fusion of the polar nuclei. The male nuclei may be easily distinguished from the nuclei of the

embryo sac by their much smaller size. This case is yet another to be added to the ever-growing list of plants in which double fertilization is known to occur.

Endosperm formation

The endosperm is initiated by cell formation. *Striga lutea* thus conforms with the type largely represented in the Sympetalae and almost universal in parasites and saprophytes (**5**).

The first division of the primary endosperm nucleus is immediately followed by the formation of a transverse wall, dividing the embyro sac into two chambers (fig. 19). The nucleus of the chalazal chamber divides once, but no wall is formed, and endosperm is never produced in this chamber. Its function is clearly haustorial, for soon after the division of the nucleus the chalazal end of the sac grows down into the integument, and finally curving upward reaches the outermost layer of the integument (fig. 22). Fig. 21 shows a somewhat earlier stage in which the remains of the antipodals are seen at the end of the haustorium.

The nucleus of the micropylar chamber divides three or four times, each division being accompanied by a wall transverse to the long axis of the sac (fig. 20). After this, walls appear in various planes and the original transverse walls are soon obscured. No definite micropylar haustorium is formed, though the cells of the endosperm grow a short distance up the micropyle, surrounding the suspensor, and are probably to be considered as having a haustorial function (fig. 23).

The endosperm cells around the suspensor (fig. 23) and those formed at the base of the original micropylar chamber (fig. 22) have dense protoplasm and stain far more deeply than the rest of the endosperm cells. This may be due to the fact that they are active in passing the food, which is gradually being absorbed from the integument by the haustoria, to the developing embryo. In these ovules there is no distinct tapetal layer round the embryo sac.

In the endosperm formation and in the development of haustoria there is a remarkably close resemblance between *Striga lutea* and *Linaria alpina*. SCHMID (**13**) in his account of *Linaria alpina* might well be describing *Striga lutea*, the chief difference being that

in *Striga* the chalazal haustorium seems to be slightly longer and to have a definite upward curve.

Embryo

After fertilization the egg cell does not divide immediately. Figs. 19 and 20 show the fertilized egg in the resting stage while endosperm is being formed rapidly.

The first division of the egg is transverse, the lower cell giving rise to the embryo, the upper to the suspensor, which develops rapidly and is divided into three or four cells by transverse walls (fig. 23). The cell of the suspensor nearest the micropyle increases in length far more rapidly than the others and crushes all the endosperm cells at its apex, thus coming to lie in contact with the integument. In appearance the proembryo is rather like that of *Physostegia* (**14**), and also, though shorter, bears a resemblance to that of *Myoporum serratum* (**3**). The cross-walls which are present in the suspensor of *Striga* and *Physostegia* are absent in *Myoporum*. A difference which becomes marked later in the development of the proembryo is the appearance of haustoria in *Striga*. These are chiefly confined to the basal cell, though in one case the cell below has produced a small lateral haustorium (fig. 26). LLOYD (**10**) in his account of the Rubiaceae shows that in many members of that family haustoria are developed from the suspensor, but as far as the writer has been able to ascertain, this has not been recorded for the Scrophulariaceae.

The embryonic haustoria are tuberous in form and do not show the slightest resemblance to those of the endosperm.

The first wall of the embryo proper is formed in a longitudinal plane (fig. 24) and is followed immediately by another longitudinal wall at right angles to the first, dividing the embryo into four cells (fig. 25). A transverse wall is then formed, dividing the embryo into octants. The next walls are periclinal (fig. 26).

Walls then follow in quick succession, giving rise to a spherical embryo (fig. 27) on the end of a long suspensor. The mature embryo is of the ordinary dicotyledonous type (fig. 28) and is surrounded by one row of endosperm cells.

Changes in endosperm and testa

At a very early stage in the formation of the endosperm, the outer wall of the outermost layer of endosperm cells becomes cutinized, and it is clearly impossible that food can pass through to the embryo, which must therefore derive its nourishment through the haustoria.

As the embryo grows, absorbing the food stored in the endosperm and integument, the walls of the outer layer of the endosperm become thickened, but are still composed of cellulose. It is these thickened cells which compose the endosperm in the mature seed. Proteid reserves alone are found, neither starch nor oil being present.

There is no well defined tapetal layer around the endosperm as is the case in most Scrophulariaceae already investigated.

All the food stored in the integument is absorbed by the haustoria and only the outermost layer of the integument persists in the mature seed. This layer undergoes a good deal of change. Its radial walls increase in size, assume a wavy outline, and become lignified. It is to this last fact that the brittleness of the testa is due.

It is a well known fact among farmers that the seed of *Striga lutea* may retain its capacity for germination for several years (**11**), owing no doubt to the protection afforded by the lignified testa and cutinized outer wall of the endosperm, as well as to the reserves of proteid material in the endosperm. When to this is added the fact that each ovary produces hundreds of seeds, practically every one of which is fertile, it is not difficult to realize why it is that this plant is so difficult to eradicate once it has obtained a hold on a crop.

Discussion

Since the middle of the last century the ovules of the Scrophulariaceae have from time to time been the object of investigation. Among the earlier workers on this subject are to be found DEECKE (**6**), TULASNE (**15**), HOFMEISTER (**9**), CHATIN (**4**), and others.

It is rather interesting to note that *Pedicularis sylvatica* was in 1855 the subject of a violent controversy between DEECKE and SCHACHT on one hand, and HOFMEISTER, VON MOHL, and TULASNE,

on the other. In 1835 SCHLEIDEN had expounded the theory that the pollen tube entered the embryo sac and there gave rise to the embryo, basing his conclusions on observations made on ovules of plants belonging to various families (**5**). In 1855 DEECKE (**6**) in *Pedicularis sylvatica* claimed to have seen the pollen tube entering the sac and developing there into the embryo, and came to the conclusion that in this plant he had proved beyond all doubt that SCHLEIDEN'S view as to the origin of the embryo was correct. SCHACHT (**12**) confirmed DEECKE'S statement, but HOFMEISTER (**9**) proved that what DEECKE had seen and drawn was the proembryo. He believed those figures in which DEECKE depicted the "pollen tube" wandering outside the micropyle to be due to roughness in dissection.

It is extremely interesting to find that the "pollen tube" of DEECKE bears a striking resemblance to the proembryo of *Striga lutea*. That it is a proembryo is obvious, since DEECKE shows it imbedded in the endosperm, and he also figures very clearly structures which in the light of SCHMID'S work on *Pedicularis* we may interpret as two lobes of a micropylar haustorium and a chalazal one. *Striga lutea* possesses a long suspensor which is clearly comparable with DEECKE'S pollen tube. In the majority of his figures the end of the "pollen tube" remote from the embryo forms a swelling much resembling that shown in the young proembryo of *Striga* (fig. 23). In DEECKE'S fig. 16 a case is shown of two "pollen tubes" entering one ovule. One of these tubes is traced down to the embryo, the other advances only a short way down the micropyle. The explanation of this phenomenon might be that in *Pedicularis sylvatica*, as in *Striga*, the basal cell of the suspensor produces haustoria and the second "pollen tube" is simply a haustorium. Of recent years the chief contributions to our knowledge of the embryo sac of the Scrophulariaceae have been made by BALICKA-IWANOWSKA (**1**) in 1899 and SCHMID (**13**) in 1906.

BALICKA-IWANOWSKA'S work is of a more general character than SCHMID'S, dealing with several sympetalous families, while SCHMID confines himself to a number of species selected from genera representing the three main groups of the Scrophulariaceae: Pseudo-

solaneae, Antirrhineae, and Rhinanthoideae. It is on this last group that most work has been done, though its subdivision Rhinanthoideae-Gerardieae, to which *Striga* belongs, has up to the present not been investigated. For this reason it is of great interest to discover how far *Striga* may be compared with the plants belonging to the Rhinanthoideae-Digitaleae and Rhinanthoideae-Rhinantheae. In all the plants which have been studied the features of the greatest interest are found in the post-fertilization phases of development and in this respect *Striga lutea* is no exception.

"Double fertilization" has been demonstrated in *Linaria vulgaris*, *Digitalis purpurea*, *Pedicularis foliosa*, and *Melampyrum silvaticum*, to which may now be added *Striga lutea*.

The development of haustoria and the development of endosperm go hand in hand and therefore may be treated together. SCHMID (13) puts the genera he has studied into four groups according to their method of endosperm formation.

In the first he puts *Verbascum*, *Scrophularia*, and *Digitalis*. In these genera four superposed primary endosperm cells are formed, of which only the two inner ones form the true endosperm, the uppermost and lowermost cells dividing into four and assuming a haustorial function, though in a much less marked degree here than is found in the other groups.

Linaria and *Antirrhinum* constitute a second group. In them a transverse division of the embryo sac occurs. The upper cell gives rise to the endosperm, of which a few cells at the micropylar end function as a haustorium; the lower cell grows out into a tube-like haustorium, in which no cell walls are formed though the original nucleus divides once.

The third group contains *Alectorolophus* (*Rhinanthus*) and part of the genus *Lathraea*, which SCHMID includes in the Scrophulariaceae. Here, as in the second group, the lower cell becomes a haustorium without septation, and two cells arising at the micropylar end of the upper cell give rise to a micropylar haustorium. Each of these cells has two nuclei.

Veronica, *Euphrasia*, *Pedicularis*, *Melampyrum*, and *Tozzia* are put in the fourth group, which differs from the third only in that

the micropylar haustorium arises from a single cell and contains four nuclei.

SCHMID has made it clear that the different species of a genus closely resemble one another in the character of the endosperm and haustoria, and he believes that these characters should receive consideration in drawing up a natural classification of the family. Judging things from this point of view, the Rhinantheae appear to be a natural group, since all the members studied show an extraordinary similarity of development. It certainly is striking that *Linaria* and *Striga*, which are widely separated in the present system of classification, should show such close agreement in their development of endosperm and haustoria. Though SCHMID has not paid much attention to the proembryo, it seems that here also is a strong resemblance. Surely there must be a close relationship between genera which show agreement in minute details of the development of organs which do not seem to be influenced by environment to nearly the same extent as those organs which are most used in drawing up a scheme of classification.

DOP (**7**) finds in *Buddleia* a remarkably close resemblance to *Verbascum*, *Scrophularia*, and *Digitalis* as regards the mode of formation of the endosperm and haustoria. He concludes that the evidence obtained emphasizes the relationship between the Scrophulariaceae and Buddleiaceae (if the latter be regarded as a family distinct from the Loganiaceae as WETTSTEIN [**16**] thinks it ought to be), and that it tends to separate the Buddleiaceae more widely from the Solanaceae.

The question whether parasitism of the plant as a whole affects the embryo sac and embryo has often been raised. The evidence afforded by the Scrophulariaceae all tends to show that these structures are not influenced by the habit of the plant. Extensive development of the haustoria is certainly characteristic of the Rhinantheae, but *Striga*, which is also a semi-parasite, is not so characterized, while *Veronica*, a non-parasite, has practically the same degree of haustorial development as the Rhinantheae. It seems, therefore, that intensity of haustorial development is not to be correlated with the parasitic habit of the plant.

BERNARD (2) was led to the same conclusion from a study of four total parasites: *Lathraea*, *Orobanche*, *Phelipaea*, and *Cytinus*, in which he found that all stages of haustorial development were represented. *Lathraea* shows the most extensive haustorial development of the four genera, while in *Cytinus* the endosperm is normal or nearly so.

In the production of fertile seeds the parasitic members of the family seem not one degree less successful than their independent relatives, and there is nothing in the history of the ovule of parasites to lead one to suppose that it has suffered owing to the mode of life adopted by the parent plant.

Summary

1. *Striga lutea* is a semi-parasitic annual belonging to the Rhinantheae-Gerardieae group of the Scrophulariaceae.

2. The ovary is of the ordinary bilocular scrophulariaceous type, and the ovules are anatropous, with one integument.

3. The megaspore mother cell arises directly from a single subepidermal cell, which gives rise to a row of four megaspores, of which the lowest develops into the embryo sac.

4. The 8-nucleate embryo sac develops in the normal way, and at the time of fertilization contains two synergids, an egg, the fused polar nuclei, which lie in the upper part of the sac, and three antipodal cells, which show signs of disintegrating.

5. Double fertilization occurs.

6. Endosperm is formed by cell division. From the chalazal end a long binucleate haustorium is formed, penetrating the integument. The micropylar haustorium is inconspicuous, simply consisting of a few ordinary endosperm cells with fairly dense contents.

7. The proembryo has a long suspensor of three or four cells. The basal cell of the suspensor forms tuberous haustoria.

8. The mature embryo is of the usual dicotyledonous type and is surrounded by one thick-walled layer of endosperm cells.

9. The testa consists of one layer of lignified cells which are admirably suited to protect the young embryo.

In conclusion I should like to take this opportunity for thanking Dr. H. H. W. PEARSON for his help during the early stages of this work, which was started at the South African College, and for his continued interest in its progress. I am indebted to Professor SEWARD for kind permission to work at the Cambridge Botany School, and to Mr. R. P. GREGORY for many helpful criticisms.

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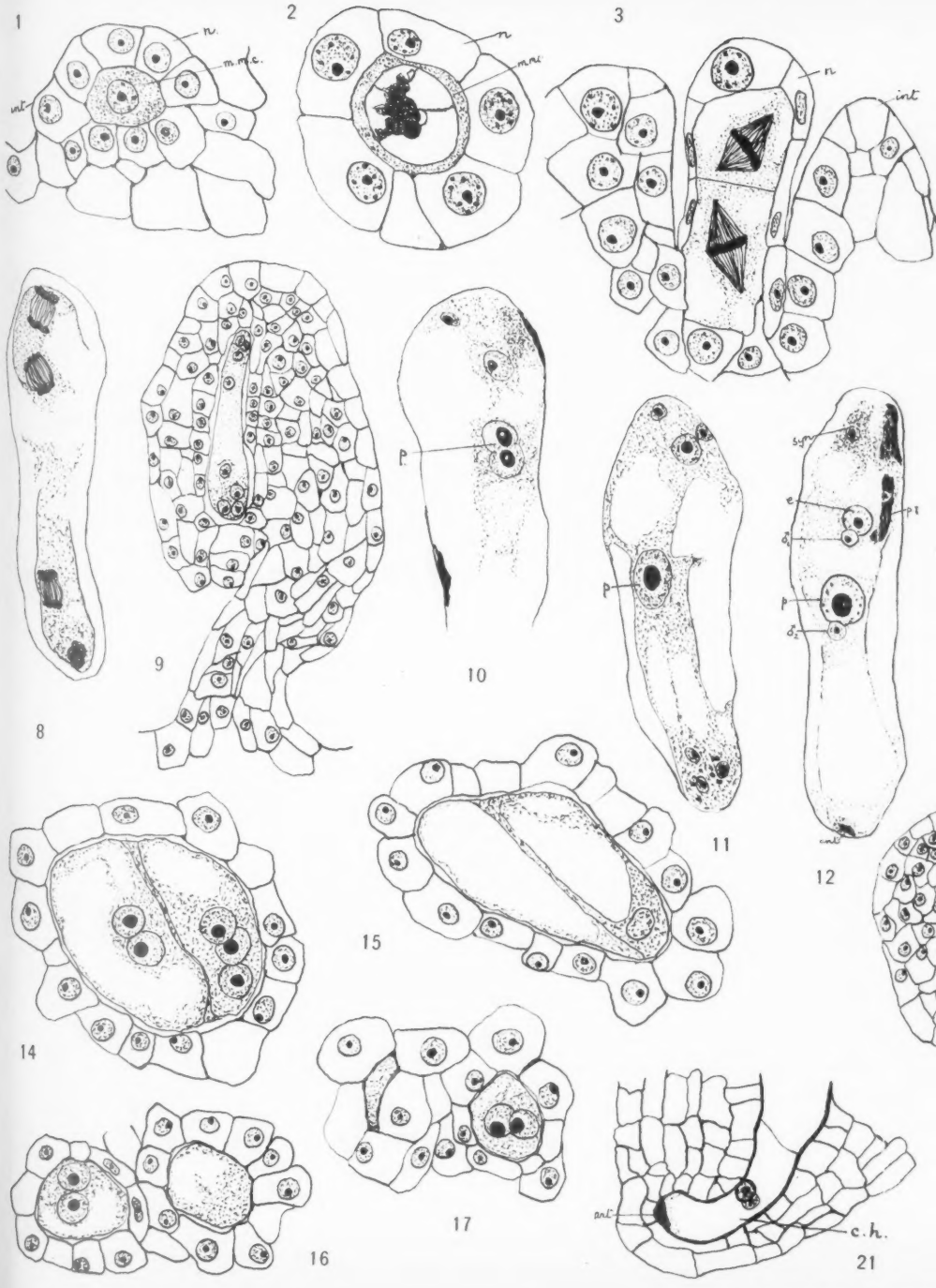
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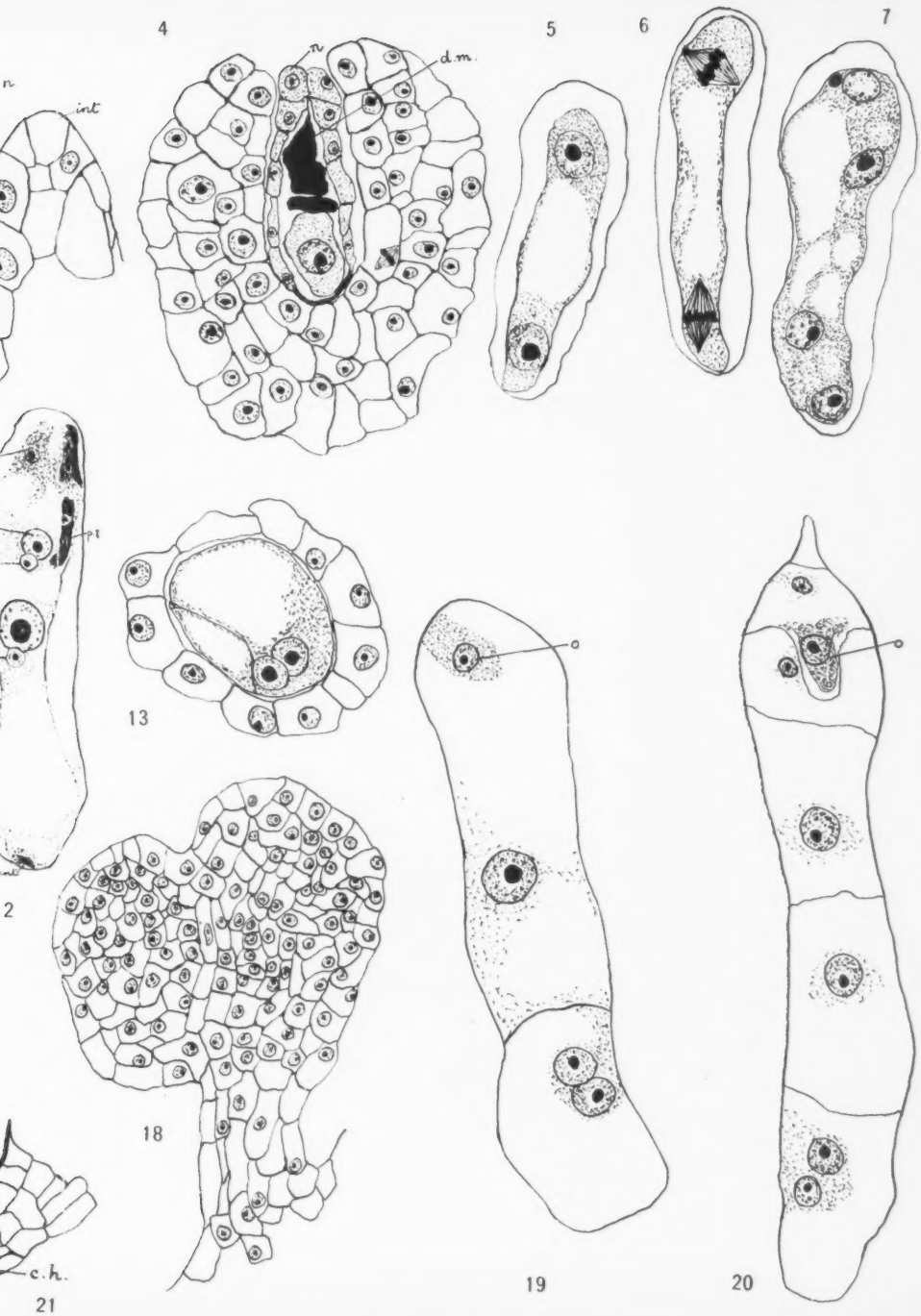
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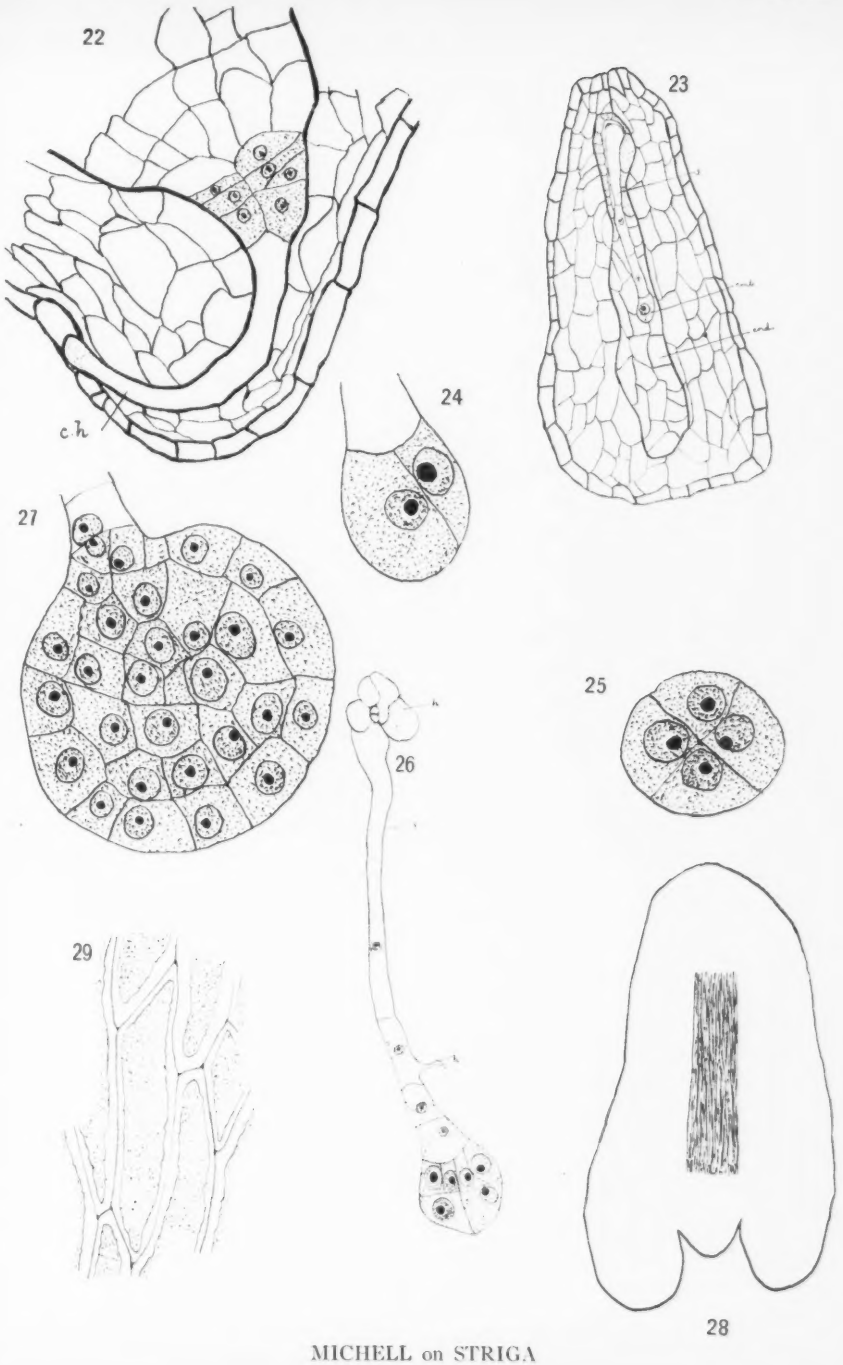

MICHELL on STRIGA

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EXPLANATION OF PLATES VIII AND IX

Abbreviations: *mmc*, megaspore mother cells; *int*, integument; *n*, nucellus; *dm*, degenerating megaspores; *p*, polars; *syn*, synergids; *ant*, antipodals; *e*, egg; *pt*, pollen tube; *o*, oospore; *ch*, chalazal haustorium; *emb*, embryo; *end*, endosperm; *s*, suspensor; *h*, haustorium.

PLATE VIII

FIG. 1.—Young ovule showing the megaspore mother cell and the origin of the integument; ×1210.

FIG. 2.—Megaspore mother cell with the nucleus in synapsis; ×1470.

FIG. 3.—Homotypic division of the megaspore mother cell nucleus; ×1470.

FIG. 4.—Ovule showing the embryo sac and three degenerate megaspores; ×1150.

FIG. 5.—Binucleate embryo sac; ×1210.

FIG. 6.—Division of the two nuclei; ×1210.

FIG. 7.—Tetranucleate sac; ×1210.

FIG. 8.—Division of the four nuclei; ×1210.

FIG. 9.—Ovule showing an 8-nucleate sac; ×1210.

FIG. 10.—Polar nuclei fusing; ×1210.

FIG. 11.—Mature embryo sac, just before fertilization; ×1210.

FIG. 12.—Fertilization; ×1210.

FIGS. 13–17.—Abnormal ovule with two embryo sacs; ×1210.

FIG. 18.—Section through this ovule not showing the embryo; ×520.

FIG. 19.—After the first divisions of the primary endosperm nucleus; ×1210.

FIG. 20.—Later stage in endosperm formation; ×1210.

FIG. 21.—Part of an ovule showing the young chalazal haustorium; ×520.

PLATE IX

FIG. 22.—Older chalazal haustorium; ×520.

FIG. 23.—Proembryo imbedded in endosperm; the chalazal haustorium cannot be seen in this section; ×260.

FIGS. 24–27.—Stages in the development of the embryo; figs. 24, 25, 27, ×1210; fig. 26, ×575.

FIG. 28.—Embryo from the mature seed; ×71.

FIG. 29.—Surface view of the testa of the ripe seed; ×605.

THE ORIGIN OF THE INFLORESCENCES OF XANTHIUM

CLIFFORD H. FARR

(WITH PLATE X)

The bur of *Xanthium*, together with the two inclosed seeds, has been the subject of considerable investigation for many years. ARTHUR (1) in 1895 confirmed the popular notion that the germination of one of the seeds is delayed approximately a year beyond the other, and also that it is the lower and better developed seed which germinates first. CROCKER'S experiments (5) in 1906 indicated that this phenomenon is due to a difference in the permeability of the seed coats to oxygen. In 1911 SHULL (14) demonstrated further that the embryos differ in the amount of oxygen required for germination; and the same writer (15) has published an article more recently on the nature of the semipermeability of the seed coats. In addition to these physiological studies, the structure of the seed coats has been investigated by HANAUSEK (10).

The morphology of the pistillate inflorescence, or bur, has been much discussed and variously interpreted. The oldest and most generally accepted view is that which considers it a fusion of involucral bracts. This was supported by WARMING (16) and ROSTOWZEW (13), and accepted by ARTHUR, GRAY, and BRITTON. As early as 1838 BRASSAI (3) dissented from this interpretation and referred to the bur as a fusion of many floral bracts. Later BAILLON (2) modified BRASSAI'S idea by assuming a union of but two floral bracts, coalesced along their margins; and GOEBEL in his most recent paper (9) accepts this explanation. However, only three years before, the last named writer (8) presented another possibility, namely, an intercalary growth about the base of the flowers, enveloping them and carrying their floral bracts upward to form the beaks.

There is also a marked difference of opinion as to the morphology of the spines which are so prominent on the mature bur. CLOS (4) suggested that these are new structures ("Emergenzen"),

and he has been followed in this by many workers, including BAILLON (2) and GOEBEL (9). However, KOEHNE (12) as long ago as 1869 conceived of them as involucral bracts; while HOFMANN (6) referred to them as "Spreublätter"; and ROSTOWZEW (13) simply called them modified bracts.

These diversities of interpretation have doubtless been due to an inadequate knowledge of organogeny, and to an incomplete correlation of the spines, bracts, etc., of related genera. A considerable number of typical Compositae have been investigated and the morphology of their parts is well established. The Ambrosiaceae, the tribe to which *Xanthium* belongs, has been excluded from the Compositae by some, though several of its genera approach very near to the typical form of Compositae. *Iva* is without doubt that member of the Ambrosiaceae most closely resembling these Compositae, and a recent discussion of *Iva xanthiifolia* Nutt. by the writer (7) involved the homology of its bracts and rudimentary structures with corresponding organs in the inflorescence of the typical Compositae. This paper also presented a hypothesis as to the origin of dicliny in that species. The present investigation was undertaken in the hope that the results of the preceding study might aid in the explanation of the dicliny in *Xanthium* and the interpretation of its peculiar pistillate inflorescence. I wish to express my appreciation for the encouragement and suggestions of Dr. R. B. WYLIE under whose supervision the work was pursued; and thanks are also due to Dr. J. C. ARTHUR for assistance in the determination of species.

The staminate inflorescence

The species investigated was *Xanthium commune* Britton, in which staminate and pistillate capitula are associated on the same branch. The staminate head, which bears 150–175 flowers, is often solitary and always terminal, thus occupying an exposed position. The peduncle (fig. 2) on which it rises above the pistillate heads is quite slender in comparison with similar structures. Its length nearly always equals or exceeds the diameter of the head which it bears; while its own diameter is only about one-sixth as great. Three vascular bundles (fig. 4) run throughout the length of the peduncle,

and the vestiges of three others appear in its lower portion (fig. 3). These vestiges suggest that the peduncle of the staminate head once possessed a more extensive vascular system. This conclusion is further supported by the larger number of bundles in the base of the pistillate head. GOEBEL (**9**), in explaining the existence of the two or three bundles in the peduncle of the staminate head of *Ambrosia*, made use of a similar hypothesis of reduction, though he presented neither of the above lines of evidence. In *Xanthium* we find that now only three bundles conduct all the water for 150 or more staminate flowers. This supply seems all the more meager when it is noted how scantily this head is protected against water loss. Only a few involucral bracts mature, and these are so small as to be of scarcely any service to the capitulum in its older stages.

The conical receptacle (fig. 1), when young, so closely resembles a developing spike that WARMING'S generally accepted theory as to the spicate origin of the capitulum is at once recalled. As in most Compositae, the marginal flowers appear first, and the apical region maintains its meristematic nature for some time. Each flower is subtended by a cylindrical or spinelike floral bract which, though furnishing slight protection, probably does not appreciably lessen the amount of transpiration.

The parts of the flower appear in centripetal order. A lobed corolla is followed by a whorl of four or five stamens, and finally a pair of carpels. About one-third to one-half of the flowers in each head have only four stamens, not even the rudiment of a fifth appearing. In flowers with five stamens the corolla always possesses five equal lobes. In those with four stamens the corolla may have either four equal or five unequal lobes. In the last case two lobes frequently represent quadrants, while the other three make up the remainder of the cycle. Evidently the primitive staminate flower of *Xanthium* was pentamerous with respect to petals and stamens. It follows, therefore, that in some cases a reduction has taken place in the number of stamens and corolla lobes, the former yielding more readily than the latter.

The stamens are always united by their filaments. Though ROSTOWZEW (**13**) and JUEL (**11**) report that the anthers never fuse, in *Xanthium commune* the adjacent anthers are sometimes joined

in the same manner as in *Iva* (**7**). The fused cutinized layer is, however, not quite as thick as in the latter form. The similarity between *Xanthium* and *Iva* further extends to the ringlike enlargement at the base of the abortive style. These facts only serve to emphasize the kinship of these two genera with the main body of the Compositae.

ROSTOWZEW (**13**) stated that the stigma of the abortive style probably does not represent two carpels. In *Iva*, though this abortive stigma is not bifid at maturity, the appearance of a notch at the apex during development indicates derivation from the typical bifid form. Since no such notch appears in *Xanthium*, it seems probable that this genus has gone one step farther and obliterated even this last clue to the evolution of this structure. The close relationship of this form of *Iva*, however, strongly suggests that this rudimentary style arose from the usual bifid form.

The pistillate inflorescence

The fertile flower is axillary, being subtended (figs. 4–6) by a leaf or another pistillate head. Many instances of aborting leaves in such relation explain the frequent absence of subtending structures at maturity. The nearly sessile capitulum is attached to the floral axis by a large base which is over twice the diameter of the peduncle of the staminate head and contains 24 bundles (fig. 5). This vascular supply, in contrast to that of the staminate head, seems remarkably extensive when it is recalled that the pistillate head bears only two flowers, while the staminate has 150 or more.

The involucral bracts, 9–15 in number, appear first and arch over the young head, protecting it very effectively. The proximal ends of the adaxial bracts are closely crowded between the receptacle and the stem, and those on the abaxial side between the receptacle and the subtending structure. Meanwhile the tips of these recurved bracts (fig. 6) come in touch with the apex of the growing receptacle near its center. It seems that this contact temporarily arrests development in that region of the receptacle, for it immediately becomes flattened. Soon continued growth of the margin of the receptacle results in the formation of an apical depression (fig. 7). It may be, of course, that this sequence of

events has become fixed in the life-history, but arrest of development in the center of the receptacle due to contact with the apices of the involucral bracts might explain its origin both in individual and racial development. In the light of the foregoing it is evident that the terminal heads develop as in the normal Compositae, because the involucral bracts are not hemmed in by subtending structures and hence their tips probably do not come in contact with the receptacle.

Growth in the marginal region is lateral as well as longitudinal, making the depression larger at the bottom and constricted above. Furthermore, the floor of the pit is never a uniformly concave surface, but is slightly elevated at its exact center (fig. 7). This elevation soon resumes growth (fig. 8) and gives rise to a septum dividing the depression into two chambers (fig. 9). Later this septum develops in its upper surface a cleft which may extend downward some distance (fig. 13).

Many papillae early cover the marginal surface of the receptacle (figs. 8 and 9), as in the staminate head. Those of the latter, it will be recalled, give rise to the flowers and floral bracts, while these papillae of the pistillate head form hard hooked spines (fig. 13). That these spines are homologous with the floral bracts of the staminate head seems reasonably certain. It is hardly likely that flowers would become transformed into such structures by any process of evolution. These spines have the form and spiral arrangement of floral bracts. Furthermore, ROSTOWZEW (**13**) has shown that the vascular anatomy is like that of bracts. To consider them new structures would be to assume the disappearance of floral bracts and the subsequent appearance of structures similar to them in exactly the same location. Such a substitution is not supported by the observed facts. It seems, therefore, that there is abundant evidence for considering these structures floral bracts.

The margin of the head grows more rapidly on one side, causing one of the depressions to become deeper. This unequal growth also accounts for the peculiarity noted by ARTHUR (**1**) that the bur is flat on one side and curved on the other. The two flowers appear simultaneously, one at the bottom of each pit (fig. 8); but the lower, being in the deeper depression, is always larger, grows more rapidly, and at all stages of development is

more advanced than the upper. This difference persists even after fertilization, and in every case the lower seed bears the larger embryo. It is evident that the lower flower is in closer connection with the vascular supply, and possibly this circumstance, together with its priority in development, may have made a difference in the nutrition and water relations of the two flowers. These factors doubtless condition to a large extent the structure and composition of the seed coats and embryo, which in turn have been shown to influence germination. It thus appears that a difference in the rate of growth of the two sides of the young head and consequently the vertical displacement of one of the seeds results ultimately in a difference in the periods of delayed germination.

The sequence of development is the same for both flowers in the bur. The abortive corolla forms at first a complete ring (fig. 10), but before maturity it disappears entirely on the outer side (fig. 11). The two carpels, though appearing later, grow more rapidly than the corolla (fig. 10), and produce the bifid stigma which projects through the beaks at the time of pollination. One instance was noted in which two collar-like structures were present, the inner reaching but half-way around the base of the style. The outer, being a complete ring, is unquestionably the normal rudimentary corolla, and the inner should doubtless be considered the vestige of an abortive whorl of stamens, such as regularly appears in *Iva* (7).

A small rudiment of a floral bract is usually noticeable on the outer side of the base of the pistillate flower (fig. 12). It will be recalled that these flowers arise in deep cavities, the walls of which crowd closely about them on all sides. There is scarcely any space for the development of a floral bract therefore, and probably this crowding accounts for its reduction to the present dwarfed condition. Its presence, nevertheless, even though much reduced, precludes the possibility of considering the beaks to be the floral bracts of the subtended flowers.

Discussion

If the bur of *Xanthium* in its individual development follows at all closely the course of its evolution, there seems no doubt of its being a modified capitulum. The involucral bracts arise in the

usual way; the floral bracts all develop into spines except those of the two inclosed flowers, which remain rudimentary; and the "Anlagen" of the two flowers which appear follow the normal sequence of development. The only respects in which this head differs from those of the typical Compositae are seen in the two beaks and the depressions which they subtend. The beaks cannot be considered as floral bracts of the subtended flowers, because the rudiments of these parts are present in the pits. Neither is it likely that they are the floral bracts of aborted flowers, for they are quite unlike the spines in form, structure, and development. The fact that they bear the spinelike floral bracts on their outer surfaces precludes their being interpreted as modified involucral bracts. Moreover, two whorls of involucral bracts have never been established for any of the Ambrosiaceae. Though some writers (**13**) have interpreted *Iva* as having a double whorl of involucral bracts, my study (**7**) has shown that the inner of these whorls might properly be regarded as the floral bracts of the pistillate flowers. It seems most reasonable, therefore, to interpret the beaks of *Xanthium*, not as modified bracts nor even as newly developed structures, but as portions of the receptacle formed by its upward growth, and slightly altered by proximity to the depressions. Under this interpretation the only modification required to transform a typical head of Compositae into a *Xanthium*-like bur is the formation of two depressions in the apical region. In this species it seems that these depressions arose, not by a sinking of the flowers into the receptacle as HOFMANN (**6**) suggests, nor by an intercalary growth in the surrounding regions, but rather by an arrest of development in the apex due possibly to contact with the tips of the involucral bracts at an early stage.

In a recent treatise on sexual differentiation in plants (**8**) GOEBEL ascribes to modifications of nutrition, not only the origin and evolution of sex, but all the phenomena of hermaphroditism, dicliny, and dioecism. He surveys the entire plant kingdom and applies his interpretation to both cryptogams and phanerogams, and to gametophyte and to sporophyte alike. Numerous experiments and observations indicate that in many cases nutrition does determine the sex of an individual or part. But, especially in the

higher plants, it is by no means certain that this is the only conditioning factor, and in some instances it seems to influence sexuality only remotely, if at all. An illustration of this last condition is found in *Iva xanthiifolia* (**7**). In it the staminate flowers seem to have been evolved by an abortion of the pistils, probably on account of exposure to excessive transpiration. On the other hand, the pistillate flowers appear to have arisen by an abortion of the stamens, brought about evidently through pressure on the terminal portion of the flower and consequently lack of space in which to develop. That such transitions could take place is evidenced by the fact that, a priori, stamens are better fitted both in structure and in function to endure desiccation than are pistils; while carpels, owing to their central (and in an epigynous flower, basal) position, are less susceptible to pressure and crowding.

Xanthium, a form with pistillate and staminate flowers in different heads, affords even stronger evidence in favor of this interpretation. In many respects the staminate flowers are more exposed to factors accelerating transpiration than are the pistillate. The staminate heads are terminal, peduncled, and not subtended by protecting leaves. Each is composed of 150 or more flowers, and is supplied by only three vascular bundles. Moreover, the flowers are borne on a highly convex receptacle, and are protected by only a few relatively small involucral bracts, while their floral bracts are mere spines. Since all these conditions are in marked contrast with those under which the pistillate flowers develop, it seems reasonable to conclude that abortion of pistils in flowers of terminal heads was due to lack of a water supply adequate for the high rate of transpiration.

On the other hand, the pistillate flowers are obviously subjected to greater lateral pressure and have only a limited space in which to develop. They occur in pits which are constricted at their openings, and are enveloped by a dense spine-covered bur. Furthermore, there is a mutual reduction of all floral appendages, including corolla, stamens, and floral bract, indicating that this abortion is due to an external cause. It seems probable, therefore, that the arrest of development in the stamens, and hence the derivation of

the pistillate flower, is a direct consequence of crowded conditions during growth.

The differences between the staminate and pistillate flowers with respect to their protection, vascular supply, and number per inflorescence have been variously interpreted. They have been considered either as secondary sexual characters, or as a direct consequence of the difference in sexuality. In the former case the characters associated with the pistillate inflorescence would be thought of as having no essential relation to the nature or function of the female sex. In the second case it would be held that the pistillate flower is protected because it is in need of protection. It is apparent that my interpretation follows neither the incidental nor the teleological views above named, but ascribes to the characters associated with each kind of flower a rôle of primary importance *in effecting* the transition from hermaphroditism to dicliny. In other words, many of the differences between pistillate and staminate flowers appeared while the flowers were still perfect; and the effects of their presence occasioned the abortion of pistils and stamens respectively, resulting in the dicliny of this species.

Ambrosia and *Franseria* resemble *Xanthium* not only in their type of dicliny, but also in the peculiar burlike female inflorescence, the principal difference being that they have but one flower in each pistillate capitulum. Although there is need of further investigation, it may be well at this time to note what relation these genera bear to the conclusions reached above. ROSTOWZEW (13) stated that the pistillate heads of both forms are found in the axils of leaves. Furthermore, GOEBEL (9), in referring to *Ambrosia*, said, "In no instance have I observed in the male capitula even a trace of a subtending bract." The vascular supply has been studied only in the peduncle of the staminate head of *Ambrosia*, in which the last named writer found only two or three bundles. It is a matter of common knowledge that in both these genera staminate heads are terminal and peduncled, while pistillate are axillary and sessile. Evidently, therefore, *Ambrosia* and *Franseria* agree closely with the conditions in *Xanthium* as regards the position, protection, and, so far as known, the vascular supply of the heads. Thus it seems likely that the foregoing interpretation of the origin

of dicliny and of the peculiar fertile inflorescence may prove applicable to other genera of the Ambrosiaceae.

Summary and conclusions

1. The pistillate and staminate heads of *Xanthium commune* may be contrasted with respect to the following characters: position, attachment, subtending structures, number of involucral bracts, number of vascular bundles in the peduncle, number of flowers, and form of receptacle.

2. The pistillate and staminate flowers differ in degree of development of pistil, corolla, and floral bract. The stamens completely abort in the pistillate flower.

3. The vascular system in the peduncle of the staminate head has doubtless undergone reduction in the number of bundles.

4. The number of stamens per staminate flower is probably now undergoing reduction.

5. The anthers occasionally fuse, indicating relationship to the typical Compositae.

6. The bur is a modified capitulum, differing from the typical head of Compositae chiefly in the two depressions in the receptacle. These pits originate through a temporary arrest of development, which may possibly be attributed to contact with the tips of the recurved involucral bracts. This recurving of the bracts may be the result of limited space due to the subtending structures.

7. The spines of the bur are probably modified floral bracts.

8. The beaks seem to be modified portions of the receptacle.

9. The terminal heads became staminate, because the vascular supply was inadequate to compensate for the excessive transpiration, and hence the pistils have aborted.

10. The axillary heads became pistillate by the abortion of stamens, owing to the pressure and crowding incident to the formation of the flowers in depressions.

11. Many of the characters in which the pistillate and staminate flowers of *Xanthium* differ have been causative factors in the origin and development of dicliny in this form.

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NOTE.—Since submitting the above for publication there has appeared an extensive study of abortive stamens by CURT SCHWARZE.[1] The author does not discuss the Compositae in this connection at all, nor does he refer to any recent work on that group. On the whole it presents very interesting corroborative evidence bearing on the conclusions reached above, when properly interpreted. Dr. SCHWARZE calls attention to SCHUMANN (1890) as the originator of the theory that reduction of stamens comes about through mutual external pressure of the organs in the bud. As opposed to this, he presents the contentions of FAMILLER (1896), MUTH, and others that abortion is due to internal factors, and himself suggests that these internal factors are constitutional in the protoplasm. This internal causation hypothesis is based on the failure in some cases to observe the parts in actual contact during development. It is evident that this is a very difficult point to demonstrate, as it necessarily involves disturbing the organs, which may itself separate surfaces loosely in contact. Moreover, recent investigations have served to greatly emphasize the delicacy of the sensitivity of plants to contact stimuli. But even granted that contact does not occur during the ontogeny of certain forms, there is still no reason that SCHUMANN and FAMILLER may not both have a correct interpretation. If we presume that the contact and mutual pressure did occur during the ontogeny of the ancestors of the living forms, such as is at present so striking in the Ambrosiaceae discussed above, it may be properly concluded with SCHUMANN that the pressure did cause an abortion. Such a reduction in size and arrest of development at an immature stage would necessarily involve a reduced vascular supply. Such a condition would doubtless result in diverted nutrition and water supply, which after many generations might make development of the stamens to maturity impossible even in the absence of mutual pressure. Thus by the reduced vascular supply becoming hereditarily fixed, there would be an internal cause for the abortion of the stamens, traceable to an original external condition. That the vascular supply is thus

[1] SCHWARZE, CURT, Vergleichende Entwicklungsgeschichtliche und histologische Untersuchungen reduzierter Staublatter. Jahrb. Wiss. Bot. **54**:183–243. 1914.

modified is indicated by the observations of SCHWARZE, in that the cells of abortive stamens are often more vacuolate than those of stamens developing to maturity.

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EXPLANATION OF PLATE X

The figures were made with a camera lucida. The magnifications given are those of the drawings before being reduced one-half in reproduction. The abbreviations used are as follows: *b*, beaks; *s*, spines; *i*, involucral bracts; *f*, floral bracts; *a*, abortive corolla; *r*, rudimentary floral bract; *p*, pistillate head; *c*, carpels; *l*, leaf; *w*, pistillate flower.

FIG. 1.—Apex of floral axis, showing a staminate head with two pistillate heads appearing at its base; ×63.

FIG. 2.—Developing staminate head; ×63.

FIG. 3.—Transverse section of lower end of peduncle of staminate head; ×70.

FIG. 4.—Transverse section of upper end of peduncle of staminate head; ×90.

FIG. 5.—Young pistillate head, showing recurved bract; ×80.

FIG. 6.—Young pistillate head, slightly older; ×80.

FIG. 7.—Young pistillate head, showing developing depression; ×120.

FIG. 8.—Young pistillate head, showing flowers appearing in the pits; ×85.

FIG. 9.—Transverse section of pistillate head with flowers partly developed; ×90.

FIG. 10.—Young pistillate flower, with carpels appearing; ×70.

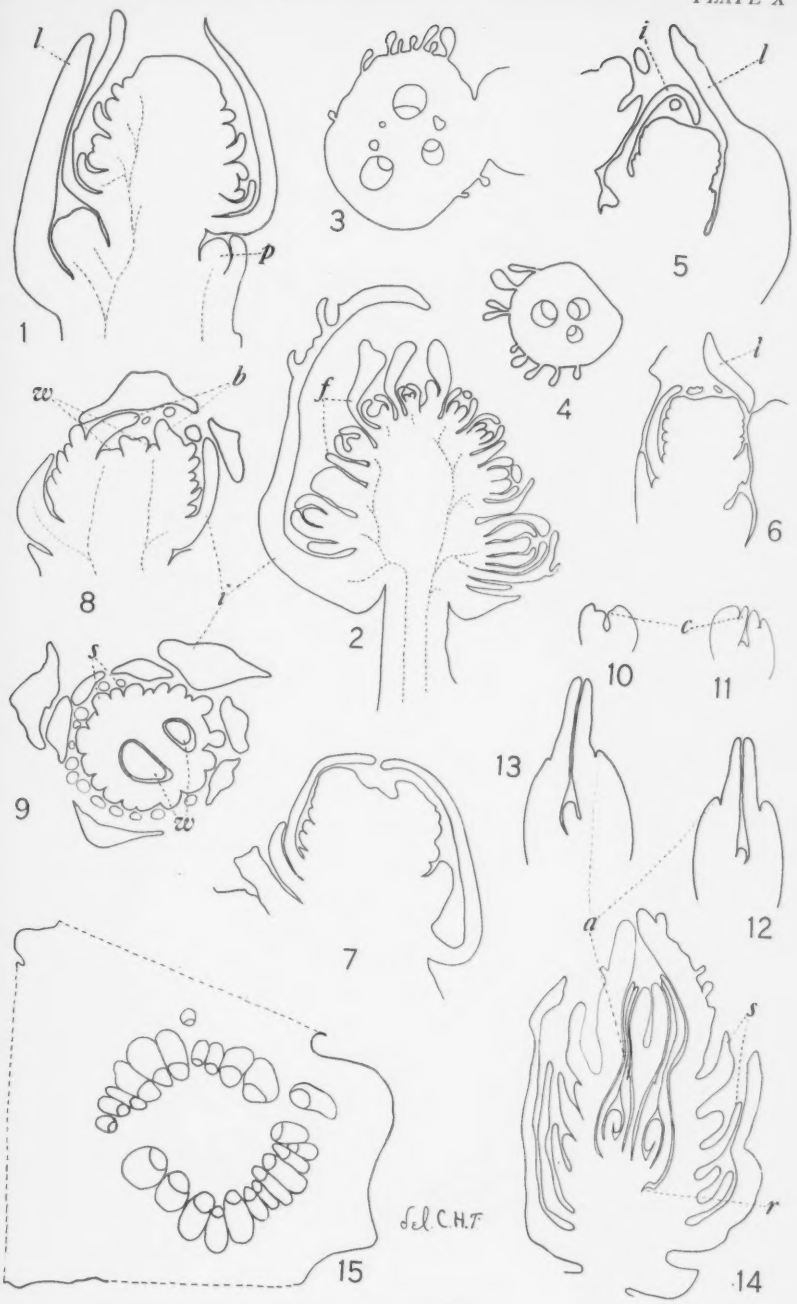
FIG. 11.—Young pistillate flower from lower pit of same head as in fig. 10; ×70.

FIG. 12.—Young pistillate flower, showing ovule appearing; ×90.

FIG. 13.—Young pistillate flower from lower pit of same head as in fig. 12; ×90.

FIG. 14.—Pistillate head at megaspore mother cell stage; ×16.

FIG. 15.—Transverse section of base of pistillate head, showing bundles; ×70.



FARR on XANTHIUM

THE VISIBLE EFFECTS OF THE SCHUMANN RAYS ON PROTOPLASM[1]

W. T. BOVIE

Since the pioneer studies of DOWNES and BLUNT, a large number of investigators have studied the effects of ultra-violet light on protoplasm. Their investigations, however, have all been made on the effect of light of wave lengths longer than 2000 Angstrom units. This paper is a preliminary report of the visible effects produced in protoplasm by light waves shorter than 2000 Angstrom units.

When studying the biological effects of light, it is convenient to divide the spectrum into the following regions:

Regions	Wave lengths in Angstrom units
Infra-red	from 10,000 to 7,200
Visible	" 7,200 " 4,000
Ultra-violet of sunlight	" 4,000 " 2,950
Quartz ultra-violet	" 2,950 " 1,850
Fluorite ultra-violet	" 1,850 " 1,250
(Schumann region	" 2,000 " 1,250)
Lyman region	" 1,250 " 900

To this series we may add Röntgen rays with wave lengths from 1 to 0.1 Angstrom units, and gamma rays with still shorter wave lengths.

The effect on protoplasm of light of the Schumann region of the spectrum is particularly interesting because in this region of the spectrum the destructive action of the light is much more violent than it is in regions of longer wave lengths. This violent action is undoubtedly connected with the fact that the Schumann region of the spectrum is a region of general absorption for nearly all substances. Even substances as transparent as air and water absorb the shortest Schumann rays. A layer of air 1 cm. thick or a layer of water only 0.5 mm.[3] thick absorbs all except the longest Schumann rays. Fluorite, the most transparent substance

[1] Preliminary communication. [2] 10,000 Angstrom units = 1 micron.

[3] LYMAN, T., Astrophysical Jour. **27**:87. 1908; Nature **84**:71. 1910.

known, is the only solid which transmits the entire Schumann spectrum. It is interesting from a biological point of view to note that the absorption bands of such substances as egg-white and gelatin begin in the longer wave lengths before we reach the Schumann region.

In the writer's observations, to be described below, unicellular organisms were exposed to the Schumann rays and observed microscopically during and after the exposure. The Schumann rays were produced by a discharge tube which was so made that it could be placed under the stage of a compound microscope in the position usually occupied by the condenser and other sub-stage attachments. When the discharge tube was in place, its fluorite window, through which the Schumann rays were emitted, was flush with the microscope stage. The Schumann light shone upward toward the microscope objective. The organisms were exposed above the discharge tube on a special microscope slide which contained a window of fluorite (glass is opaque to these rays). The regular sub-stage attachments could then be swung into place and the organisms observed under high magnifications.

The effects produced by the light were immediate. There was a marked stimulation, followed by cytolysis, which, with a sufficient exposure, terminated in death. All of these changes were usually produced by an exposure of less than one minute's duration.

It was found that a given amount of exposure to the light produced the same effect whether the exposure were continuous or interrupted. This made it convenient to interrupt the exposure from time to time and to make a detailed study of the progress of the changes produced by the light.

The temperature of the drop of water containing the organisms was measured by means of a thermal junction, the variable junction of which was placed beside the organisms under the coverglass. As the temperature did not rise 1° C. during the experiment, the changes produced could not have been due to heat.

The length of time required for killing varied both with the species and with the individual organisms. In general, a small

organism was killed more quickly than a large one. With a given intensity of light, an exposure of several minutes was not sufficient to kill such organisms as rotifers and minute worms, while *Sphaerella*-like swarmspores, which contain both chlorophyll and an "eye-spot," were killed almost instantly. The swarmspores were killed so quickly that there was not sufficient change in temperature to be indicated by the thermal junction. The protoplasm of the swarmspores which had been killed by the light had a granular appearance. Often some of the protoplasm was extruded from the cell and was rounded up into drops.

The cells of a large *Spirogyra* of the *crassa* type were killed by an exposure of 45 seconds when the discharge tube was carrying 18 milliamperes. The various cell organs were affected quite differently by the exposure to the light; for instance, the nucleus became enlarged, while the chlorophyll bands contracted about it and became disorganized.

Active amoebae often showed very marked negative phototropism. The tips of their extended pseudopodia usually turned upward away from the light. Often a pseudopodium was pushed up from the upper surface of the body. The nucleus, together with a large portion of the granular endoplasm, flowed into this pseudopodium, leaving a clear ectoplasm below. With an amoeba in this condition, a properly timed exposure killed all of the lower part without killing the upper part; so that after the exposure, the protoplasm contained in the vertical pseudopodium moved away, leaving the coagulated lower part behind. In some cases, so much of the protoplasm flowed up into the pseudopodium that the amoeba became too heavy and toppled over. One amoeba was seen to send up a pseudopodium, to fall over, and then to repeat the process three times before it was killed.

Under the influence of the Schumann rays the endoplasm contracted, so that there appeared to be an increase in the amount of ectoplasm. The line separating the endoplasm from the ectoplasm was sharply defined. After a prolonged exposure, there was often a peculiar flowing of the granular endoplasm out into the ectoplasm. It did not appear to be the same kind of motion which one observes in the regular streaming of the protoplasm, but it was not easy to

say wherein the difference lay. After this all motion ceased and the protoplasm appeared coagulated. Under a high magnification (2200 diameters) the protoplasm was seen to be filled with small vacuoles which were so numerous that it had the appearance of a fine froth. These vacuoles were not visible before the organism was exposed to the light.

The length of exposure necessary to bring about these changes varied from 30 to 100 seconds when the hydrogen discharge tube was carrying 29 milliamperes. Since the effect on the organisms is additive, the entire exposure was not made at one time, but at intervals, so that the experiment often extended over an hour. Thus the changes produced by the light could be more carefully observed.

Infusoria are very quickly cytolyzed by the rapid vibrations of these ultra-violet rays. The nature of the cytolysis varies greatly with the species, and, in some of the minor details, it varies with different individuals.

The writer has observed three kinds of photo-cytolysis in ciliated infusoria: first, a cytolysis which is accompanied by the formation of vesicles on the surface; second, a cytolysis in which some of the internal portions of the protoplasm coagulate; and, third, a cytolysis in which some of the protoplasm disintegrates directly. The first two types of cytolysis were observed in *Colpoda*-like forms, and the third type was observed in *Stylonychia*.

The cytolysis by vesicle formation requires an exposure of about 30 seconds when the discharge tube is carrying 18 milliamperes. The vesicles are filled with a clear liquid and are often as large as the organism itself. Several vesicles may form and again disappear during the exposure. With sufficient exposure, the surface which separates the protoplasm from the fluid contained within the vesicle breaks, and the protoplasm flows out into the vesicle. A still longer exposure may cause the outer wall of the vesicle to rupture. The protoplasm then flows out into the surrounding water, with which it is miscible.

In the cytolysis in which parts of the protoplasm coagulate, an exposure of a few seconds results in the formation of small masses of coagulum, which are at once extruded by the organism. Con-

tinued exposure causes these coagulated masses to form faster than they are extruded. Soon a swelling appears, which bursts, and the protoplasm flows out.

In *Stylonychia*, the protoplasm disintegrates directly, and becomes miscible with the surrounding water. If the current of the discharge tube is increased to 60 or 70 milliamperes the disintegration begins at once. The infusorian darts across the field, leaving a trail of its cytolyzed protoplasm behind. The organism continues to move until only a few cilia with an attached mass of protoplasm is left intact, and this cytolyzes the instant motion ceases.

When thin-walled fungous spores are exposed to the light, the protoplasm either takes on a coagulated appearance, or the spore bursts. The spores which burst explode with such force that they are shot backward by the reaction. After the explosion a small mass of coagulated protoplasm is seen lying near the exploded spore.

This brief description of the visible effects of the Schumann rays is sufficient to indicate that these ultra-violet light rays have a most violent effect upon protoplasm. The writer has demonstrated by methods not described in this paper that the effect of the light is upon the organism itself and not upon the surrounding medium.

Vesicle formation and the bursting of spores point strongly to changes in osmotic relations or in imbition, which may be connected with the fact, as shown in a previous paper,[4] that the longer ultra-violet light waves have the power to break down proteins. It will undoubtedly be found that these rays have a similar, and, judging from the violence of their action, a much greater power.

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[4] Science N.S. **37**: 24. 1913.

FLOWER OF ADENOCAULON BICOLOR

JESSIE A. AYRES

(WITH PLATES XI AND XII)

Adenocaulon bicolor Hook. is distributed from the Himalaya Mountains to Japan, and from the northwestern part of the United States to Lake Superior. The only other species is *A. chilenae* Less., from Chile to the Straits of Magellan. The plant is a peculiar one, having no pappus, but an abundance of glandular hairs on the seed. This work was undertaken under the direction of Dr. T. C. FRYE of the University of Washington, with the object of comparing the development of the staminate and pistillate flowers.

The heads are arranged in a raceme (fig. 1), which appears as a swelling between the upper leaves (fig. 2, *s*). On this swelling cycles of protuberances appear (fig. 3, *a*, *c*), which become the bracts of the inflorescence subtending the peduncles; but the uppermost whorl becomes the involucre of the terminal head (*c* in figs. 4–9). When the involucre arches over the head, the primordia of the individual flowers appear as bulges on the receptacle (figs. 6 and 7, r^1, r^2). Some of the primordia divide, thus increasing the number of flowers (figs. 8–10, *x*). This mode of increasing the number of flowers suggests a tendency in the heads to branch, and points toward a probable ancestral form with scattered flowers. The axillary heads appear shortly after their bracts arise (fig. 9, *b*). The flowers develop in acropetal succession, as do the parts of the individual flowers (fig. 10).

In the staminate flowers, when the floral parts begin to develop, the flower primordia first broaden at the top (fig. 9, *p*). The corolla then appears as a marginal ring (fig. 10, *mr*) on the top. After the corolla tube lengthens and begins to curve inward, a ring of small bulges appears in the throat of the tube; these are the beginnings of the stamens (fig. 10, *st*). When the stamens are well started, the carpels appear beneath them (fig. 11, r^2, *ca*). Thus all the normal parts except the calyx are present (fig. 12, r^2). When the bundle enters the staminate flower, it separates into a

whorl of five strands about a central strand. The latter terminates at the base of the sterile ovarian cavity; while the five strands about it pass up about the ovarian cavity until they reach half of its length (fig. 13, b^1). Then the two of these strands which are opposite to the two lobes of the stigma branch (fig. 13, b^2), each branch passing up into a lobe of the stigma. The main branch of each of these two strands and also the three other main strands pass up into the corolla, where each branches just below the base of its opposite stamen (fig. 13, b^3); one branch passes up into the stamen, and the main one continues up into the apex of the corolla. The fact that the stigma is cleft does not agree with descriptions in ENGLER and PRANTL'S *Die natürlichen Pflanzenfamilien*, BRITTON and BROWN'S *Illustrated flora*, and HOWELL'S *Flora of Northwest America*.

In the pistillate flower the history is the same up to the development of the ovarian cavity. When the base of this cavity broadens (fig. 12, r^1, *oc*), a bulge appears, which is the beginning of the ovule.

The megaspore mother cell is formed in the usual way, and occupies all or nearly all of the outer end of the nucellus. Behind the megaspore there is crowded a row of two or three other rather large cells, which gives the appearance of a row of three or four megaspores. Sometimes other cells remain at the side of the mother cell, and the outermost ones are often elongated and resemble the mother cell in size but not in content (fig. 14, *nu*). The megaspore mother cell passes through the usual two successive divisions, and the inner megaspore becomes the embryo sac (fig. 21). The embryo goes through the same phases of cleavage (fig. 22) as those reported by MERRELL[1] in *Silphium*.

When the megaspore mother cell has enlarged (fig. 14), the first gland-hairs appear on the akene. Usually the first glands appear just where one would expect a calyx. This leads one to suspect that the tendency of the cells at that point to form projections is still slightly more marked than at other points. These glands develop from a protrusion of four epidermal cells of the akene. These cells are large and have large nuclei (fig. 15). They elongate and form a knob on the end (figs. 15–19). Many more glands

[1] BOT. GAZ. 29:115–124. 1900.

appear shortly after the first ones. In the mature plant the whole inflorescence and the upper part of the stem is glandular, but no glands appear at all on the staminate flowers.

The paths of the axial bundles are the same as those in the staminate flowers, with two exceptions: first, the strand in the center of the whorl of five strands at the base of the ovarian cavity is not abortive, but passes into the ovule and curves with the integument to a point level with the antipodal cells (fig. 20, *a*); second, even when there are stamens no branch of the upper corolla strand branches into them. After fertilization, the style and corolla wither and drop off. When this happens, the whorl of five strands which lies adjacent to the integument (fig. 20, *b*) disorganizes and disappears, along with tissues which are also adjacent to the integument, thus freeing the ovary from the integument.

The style is cleft (fig. 20, *sti*) and the stigma is covered with papillae like those on the staminate flowers.

When the ovarian cavity begins to develop, the growth of the stamens is retarded. Usually they disappear, but sometimes remain as seen in fig. 20, *st*, but none bearing pollen sacs were seen.

There was nothing unusual found in the formation of pollen grains. The outer wall layer becomes thick and spiny, while the spore becomes winged. In grooves between the wings, the extine is merely in contact. At the three germinative spots the walls are pushed outward (fig. 23). This occurs before the pollen grains leave the anther.

Summary

The development of the staminate and pistillate flowers is the same up to the development of the ovarian cavity.

Both staminate and pistillate flowers have ovarian cavities, but ovules develop only in the pistillate flowers.

Stamens are sometimes found in pistillate flowers, but they are always sterile.

No gland-hairs are found on staminate flowers.

Styles of staminate flowers are cleft.

Nothing unusual occurs in the development of the egg, embryo, or pollen grains.

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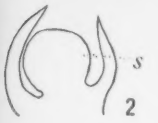

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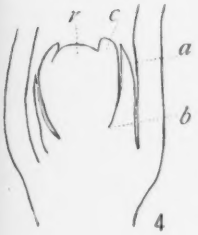

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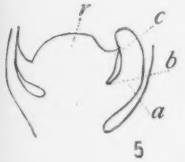

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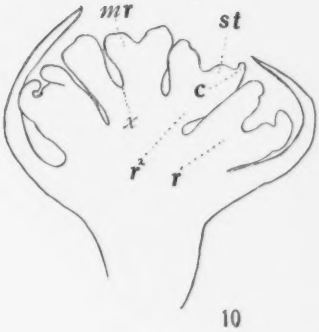

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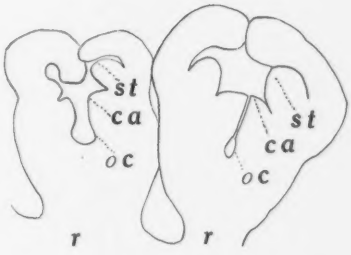

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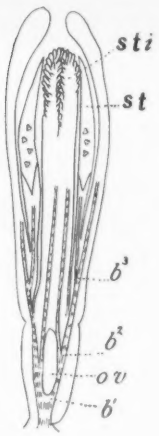
AYRES on ADENOCAULON



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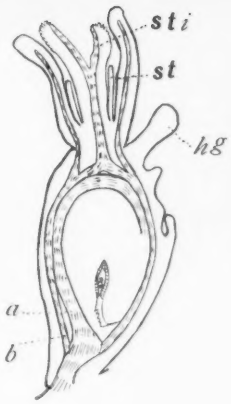

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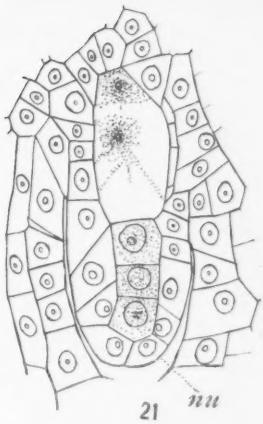

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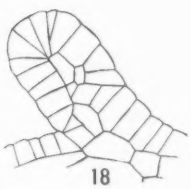

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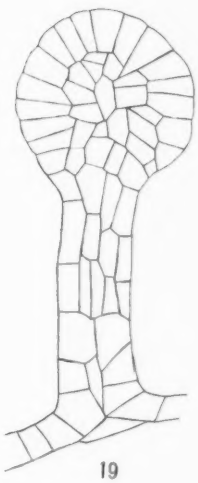

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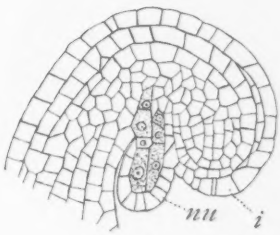

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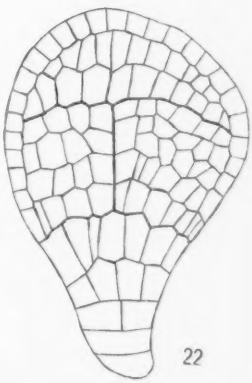

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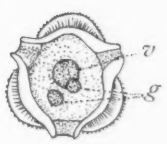

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AYERS on ADENOCAULON

EXPLANATION OF PLATES XI AND XII

All figures except fig. 1 were made with a Bausch and Lomb camera lucida. The plates are reduced to one-half of the original size. The magnifications are for the drawings as reduced.

PLATE XI

All figures (except fig. 1) ×77.5

FIG. 1.—A mature inflorescence; ×8.

FIG. 2.—The first appearance of raceme between upper leaves (*s*).

FIG. 3.—First appearance of bracts of raceme (*a* and *c*); *b*, axis of bract; *r*, receptacle of terminal head.

FIGS. 4 and 5.—Further development of raceme.

FIG. 6.—First appearance of flower primordia (r^1 and r^2).

FIG. 7.—Further development of flower primordia.

FIG. 8.—A primordium dividing (*x*).

FIG. 9.—Further division of primordium (*x*); *p*, widening of top of staminate flower; *c*, involucral bract; *b*, axillary head; *a*, bract of the inflorescence.

FIG. 10.—Inflorescence completed: *x*, division of a primordium almost completed; r^2, staminate flower; r^1, pistillate flower; *mr*, first appearance of corolla by a marginal ring; *c*, corolla in more advanced stage; *st*, stamen.

FIG. 11.—Further development of staminate (r^2) and pistillate (r^1) flowers: *c*, corolla; *st*, stamens; *ca*, carpels.

FIG. 12.—Further development of fig. 11: *oc*, ovarian cavity; other parts labeled as in fig. 11.

PLATE XII

FIG. 13.—A developed staminate flower: *sti*, stigma; *st*, stamen; *oc*, ovarian cavity; b^1, b^2, and b^3, branching points of the bundles; ×30.

FIG. 14.—Ovule: *i*, integument enveloping megaspore mother cell; a cell of the nucellus still remaining parallel to the megaspore mother cell; *nu*, nucellus; ×335.

FIG. 15.—First appearance of gland-hairs by the elongation of epidermal cells; ×335.

FIGS. 16–18.—Development of gland-hairs; ×335.

FIG. 19.—Developed gland; ×250.

FIG. 20.—A mature pistillate flower showing path of the bundles: *sti*, cleft stigma; *st*, sterile stamen; ×30.

FIG. 21.—Inner megaspore has become the embryo sac, and its nucleus has passed through the first stage of division; *nu*, nucellus; ×766.5.

FIG. 22.—Older embryo; ×550.

FIG. 23.—Details of the extine and intine: three germination spots; *v*, vegetative nucleus; *g*, two male cells; ×766.5.

CURRENT LITERATURE

MINOR NOTICES

Submerged forests.—People invariably are fascinated by evidences of former forests below present sea-levels, as indicated by the appearance at low tide of stumps *in situ*. That these "Noah's woods" are of large scientific interest is well brought out in an interesting little booklet by CLEMENT REID, forming one of the useful series of "Cambridge Manuals of Science and Literature."[1] REID speaks in detail of the various submerged forests of the English coast and of the Dogger Banks in the North Sea. The lowest of these forests are oak forests much like those of the present day, though apparently with fewer species. Among the species absent are the more southern types that have come into England since the ice age; at the same time, the glacial relicts have disappeared. It is concluded that the lowest of these forests date back about 5000 years, and that there has been no essential change of sea-level in the last 3500 years. During the period of the life of these forests the climate was much like that of the present, and the land was 60–90 feet higher than it is today.

In connection with REID's book on submerged forests, attention may be called to a short paper by OSBORN, dealing with a submerged forest on the coast of Wales.[2]—H. C. COWLES.

Plant evolution.—CAMPBELL[3] has presented an interesting popular account of plant evolution for the "American Nature Series." Following a brief consideration of the factors in evolution, the different plant groups are considered, from the bacteria and blue-green algae through the angiosperms, the object here being to set forth the chief characters of each group in the scale of ascent. The book closes with four chapters having the following titles: environment and adaptation, the problems of plant distribution, the human factor in evolution, and the origin of species. Since most books of this character deal with animals rather than with plants, this volume of CAMPBELL's is especially welcome.—H. C. COWLES.

[1] REID, CLEMENT, Submerged forests. pp. 129. *figs. 4* and *frontispiece*. Cambridge University Press. 1913.

[2] OSBORN, T. G. B., A note on the submerged forest at Llanaber, Barmouth. pp. 10. *figs. 2. pls. 2*. Reprint from Mem. Proc. Manchester Lit. Phil. Soc. **56**: 1912.

[3] CAMPBELL, D. H., Plant life and evolution. 8vo. pp. iv+360. *figs. 22*. New York: Henry Holt & Co. 1911. $1.60.

NOTES FOR STUDENTS

The vegetation of Connecticut.—NICHOLS[4] has published the first three papers of a contemplated series detailing the various ecological features of the vegetation of Connecticut. The first of these papers deals with general phytogeographic features, both floristic and ecological. The most interesting floristic problem considered is the segregation in the southeastern part of the state of many characteristic coastal plain plants. Some of these plants are confined to the southeastern part of the state, and the rest are decidedly more frequent there. One of the most important of the latter class is *Chamaecyparis thyoides*, the chief character plant of the "cedar swamps"; associated with this is *Rhododendron maximum*. Since these coastal plain plants are found more or less continuously along Long Island, NICHOLS favors the theory of a postglacial land bridge connecting eastern Long Island with the mainland, as suggested by HOLLICK. The climax forest of the state is very mesophytic and is composed of several deciduous trees (chestnut, white oak, red oak, sugar maple, red maple, beech, tulip, linden, etc.) with the hemlock. The forests in the hilly regions of northwestern Connecticut contain the spruce, fir, and other forms that are strikingly more boreal than are the coastal plain plants of southeastern Connecticut. After giving brief consideration to maritime and some other associations, NICHOLS notes a few of the cases of eccentric distribution in the state; a notable instance is that of a moss, *Claopodium pellucinerve*, which is known elsewhere only from the Yukon Territory and India. The first paper closes with an account of the climate and physiography of the state.

The second paper is devoted to a consideration of the virgin forests of Connecticut. Much the finest of these was the recently destroyed Phelps forest in Colebrook, in the northwestern part of the state. So far as known, this forest of 300 acres dates back to prehistoric days, almost unmodified by the ax or by fire. It is taken to be the dominating type of forest in the state, up to the time of settlement by the white man, and may be regarded as the best example of a climax forest in Connecticut. *Fagus grandifolia* and *Tsuga canadensis* make up 55 per cent of the stand. *Acer saccharum* and *Betula lutea* comprise 22 per cent. The remaining 23 per cent is made up of *Quercus rubra, Castanea dentata, Fraxinus americana, Tilia americana, Prunus serotina, Betula lenta, Acer rubrum*, and *Pinus Strobus*. Some of the trees are of immense size, and it is noted that the same species form the undergrowth. There is a rich undergrowth of shrubs, in which a large part is played by *Taxus canadensis, Viburnum alnifolium*, and *Kalmia latifolia*. The liverwort and moss flora are astonishingly rich. It is a matter of profound regret that this beautiful and unique forest was destroyed in 1912, so that the last extensive primeval woodland of the state has gone. NICHOLS is to be congratulated upon having made a record

[4] NICHOLS, G. E., The vegetation of Connecticut. I. Phytogeographical aspects. II. Virgin forests. III. Plant societies on uplands. Torreya **13**:89–112. *figs. 6;* 199–215. *figs. 5.* 1913; **14**:167–194. *figs. 9.* 1914.

of its plant population before it was too late. Three fragments of primeval forest are noted in the same part of the state. The population is much the same as that of the Colebrook forest, except that the one in Cornwall is dominated by *Pinus Strobus;* these pines are said to be the most magnificent still existing in the East. The pine is not the climax type, however, since the undergrowth is dominated by hemlock and several hardwoods.

In a third paper, NICHOLS details the successional relations of the upland vegetation of the state. One of the most characteristic rock types of Connecticut is the trap ridge, whose vegetational history is depicted from the pioneer crustose lichens through the herb, shrub, and tree stages. Early trees are *Juniperus virginiana* and *Quercus stellata*, following which *Carya glabra* and *Quercus Prinus* are likely to prevail. These form a somewhat open forest, which later develops into a closed forest, dominated by several species of oak and hickory. This or a more mesophytic forest represents the climax type. The trap ridges have very characteristic talus slopes, on which the vegetation passes rather rapidly to the mesophytic climax forest. Another interesting upland succession is that of the sand plains, on which one of the prominent early tree stages is dominated by *Pinus rigida*, which later is succeeded by oaks. In the state are many abandoned fields which are reverting to forest, an early stage being that dominated usually by *Betula populifolia*, *Juniperus virginiana*, and *J. communis depressa*. Note is made of the varying importance of certain trees in different portions of the state; *Pinus Strobus* is of special interest in this respect, being a common pioneer in some parts, almost a climax tree in other parts, and negligible in still other parts. The importance of the chestnut in many Connecticut woodlands is being greatly lessened, owing to the ravages of the chestnut bark fungus, *Endothia gyrosa parasitica*.—H. C. COWLES.

Inheritance of semi-sterility.—BELLING[5] has made a careful analysis of the inheritance of partial sterility in crosses of *Stizolobium deeringianum* Bort. (Florida velvet bean) with other species of the same genus, namely *S. niveum* (Roxburgh) Kuntze (Lyon bean), *S. hassjoo* Piper and Tracy (Yokohama bean), and *S. niveum* var. (China bean). The pollen from healthy flowers of all these forms was found to be nearly 100 per cent good. A few ovules of some pods only were found to have aborted, due, the author believes, to circumstances unfavorable for those particular pods. From a third to a half of the pods had no aborted ovules. The ovules in general had completely formed embryo sacs. Of the F_1 generation of the three crosses, approximately 50 per cent of the pollen grains were found to be shrunken and non-viable, the other 50 per cent being perfectly developed and viable. Similarly, approximately 50 per cent of the ovules of F_1 plants abort. Sections of young ovaries

[5] BELLING, JOHN, The mode of inheritance of semi-sterility in the offspring of certain hybrid plants. Zeitschr. Ind. Abs.- u. Vererbungs. 12:303–342. 1914.

showed almost exactly one-half of the ovules with complete embryo sacs "nearly filling the nucellus," while the other ovules, "though full sized, had either quite aborted embryo sacs, the nucellus being a uniformly cellular mass, in which, however, the remains of the aborted megaspore could usually be distinguished, or had only a minute cavity to represent the embryo sac." The fact that somewhat less than half the seeds of ripe pods were found to have aborted is believed to be due to a selective elimination through dropping of young pods that chanced to have all or nearly all aborted ovules. In the F_2 generation about one-half of the plants had almost wholly normal pollen grains and in the other half approximately 50 per cent of their pollen grains aborted as in F_1. The F_2 plants with normal pollen also had few aborted ovules just as the parent species had, while those with semi-sterile pollen had about 50 per cent aborted ovules. The F_3 progenies of fertile F_2 plants were wholly fertile. The semi-sterile F_2 plants, like all F_1 plants, produced F_3 offspring a half of whose members were fertile and a half semi-sterile with regard to both pollen and ovules. Some of the fertile F_3 stocks were grown on a large scale and found to breed true to that characteristic in F_4 and F_5.

The author points out clearly that the form of sterility observed in *Stizolobium* hybrids manifests itself only in the haploid, never in the diploid generation. The F_2 ratio of 1:1 from selfed F_1 plants is not, therefore, a zygotic but rather a gametic ratio. It is interpreted accordingly as simple Mendelian segregation, exceptional only in that the segregation is here visible in the gametes themselves and not merely inferred from the appearance and behavior of the zygotes as in ordinary Mendelian cases. Since gametes are haploid (simplex for genetic factors), it is obvious that dominance and recessiveness, either complete or partial, cannot in any way be concerned in this problem. As a working hypothesis, the author assumes two genetic factors, *K* and *L*, one present in *S. deeringianum* and the other in each of the other species. It is assumed that the presence of one or the other of these factors is essential for the development of normal pollen grains and embryo sacs, but that in the presence of both factors, just as in the absence of both, no development results. The hypothesis accounts for all the facts observed. The author promises the further crucial test of crossing together different fertile lines from the progeny of semi-sterile plants, in which, if the hypothesis holds, half of the crosses should yield only fertile and half only semi-sterile offspring. It would be instructive also to cross together the three forms other than *S. deeringianum*, all of which should produce wholly fertile hybrids.

It remains only to be said that, as an alternative hypothesis, *K* and *L* might be regarded as inhibitors of complete gametic development when present singly, the one neutralizing the effect of the other when both are together. *KL* and *kl* would then result in normal and *Kl* and *kL* in aborted gametes, just the reverse of the author's assumption. Both assumptions are equally in accord with the observed facts and the same further results are to be predicted from both. The author is to be congratulated upon the thoroughness of his

analysis and the clearness of its presentation. The excellent illustrations accompanying the paper add not a little to its effectiveness.—R. A. EMERSON.

Calcicoles.—MALCOLM WILSON[6] has made a study of the varying composition of the woodlands of southeastern England, in connection with variations in the substratum. His conclusions are in harmony with those of most English ecologists, namely that the flora of the chalk and of other calcareous strata differs considerably from that overlying non-calcareous strata. However, the vegetation on the siliceous London clay differs considerably from that on the very similar "clay with flints," whereas the latter has a vegetation much like that of the chalk. Parallel species are found on the chalk and the clay with flints, the former being more xerophytic in structure; these results agree with those found long ago by KERNER. WILSON shows how other factors, such as depth of soil and amount of shade, are as likely to be limiting factors as is soil composition. These woodlands are largely coppiced every fourteen years or thereabouts, and WILSON pays large attention to the changes brought about at coppicing, through the admission of light, and to the gradual changes later on, as shade increasingly returns. While shade-tolerant species gradually get the upper hand in the years following coppicing, it is interesting to note that certain perennial species, usually regarded as light-requiring, may remain through the shade period; these plants are dwarf in habit and reproduce only vegetatively.

As is well known, most American ecologists place little emphasis on the division of plants into calcicoles, silicicoles, etc. BUTTERS,[7] however, records from the Selkirk Mountains of British Columbia some observations that harmonize well with the calcicole theory proposed by UNGER in 1836. One of the lateral moraines of the Sir Sandford glacier is composed chiefly of fragments of limestone and dolomite, whereas the other lateral moraine is composed chiefly of fragments of granite and mica schist. The flora of these two moraines is strikingly different, only 34 of the entire 110 species occurring on both moraines; only 21 species occur somewhat equally in the two habitats. The flora of the limestone moraine is composed of species that are largely rare or local in the Selkirks, and it is to be noted also that limestones are similarly infrequent in these mountains. All other limiting factors seem excluded except that of difference in chemical composition of the substratum. There are 34 species on these moraines, which were found in eastern North America by FERNALD;[8] 20 of these have exactly the same type of soil distribution in these widely separated regions, and in no case is there a reversal of soil preference.

[6] WILSON, MALCOLM, Plant distribution in the woods of northeast Kent. I. Ann. Botany **25**:857–902. *figs. 4. pls. 3.* 1911.

[7] BUTTERS, F. K., Some peculiar cases of plant distribution in the Selkirk Mountains, British Columbia. Minn. Bot. Studies **3** and **4**:313–331. *fig. 1.* 1914.

[8] See BOT. GAZ. **45**:138–139. 1908.

For fifty years, commencing with KERNER, many European botanists have called attention to the relatively xerophytic features of limestone plants. HOSSEUS[9] shows that these same features hold for the tropics. His studies were made on a mountain in northern Siam, and he records the following xerophytic habits as characteristic: shortened, lignified, much-branched stems; reduced leaf surfaces; involute leaves; succulence, etc.—H. C. COWLES.

The chestnut disease.—ANDERSON and RANKIN[10] have published a bulletin upon the chestnut disease which has attracted so much attention. The bulletin brings together the scattered data in reference to the disease and presents the known facts in a very convenient form. It seems that this "canker" was first discovered by MERKEL in 1904 on the American chestnut in the New York Zoological Park. The rapidity of spread has been phenomenal, and the authors state that "the completeness of destruction is without parallel in the annals of plant pathology." The latest published information states that the disease is now generally distributed among native chestnuts from New Hampshire and the Hudson region of northern New York to Virginia; and has spread westward into New York and Pennsylvania, but has not yet been found in Ohio or Indiana.

The name of the causal organism has been under considerable discussion, and the various views are presented. The authors adopt *Endothia parasitica* (Murr.) Anders. The morphology is discussed in detail, treating of stromata, pycnidia, pycnospores, perithecia, asci, ascospores, and mycelium. It is obvious that the American chestnut (*Castanea dentata*) is by far the most susceptible host, but no species of *Castanea* has been proved to be immune, although some of the oriental varieties show a certain amount of resistance. The conclusion at present is that this disease is not a serious menace to any forest tree except the chestnut. The problem of dissemination is discussed in detail, including such factors as man, insects, rain, birds, wind, and other minor agencies.

Naturally the subject of control is discussed with all available data, and the general conclusion is reached that "at present we know of nothing that will prevent the extermination of the American chestnut tree." The authors, however, "do not believe that the ingenuity of our scientists has been exhausted," a hopeful belief which we trust will be justified.—J. M. C.

Morphology of Peperomia hispidula.—JOHNSON[11] has made a detailed study of this species, having a very simple vegetative structure and a peculiar

[9] HOSSEUS, C. C., Edaphische Wirkungen des Kalkes auf die Vegetation tropischer Karren und Karrenfelder. Bot. Jahrb. **45**:661–669. 1911.

[10] ANDERSON, P. J., and RANKIN, W. H., *Endothia* canker of chestnut. Cornell Univ. Agric. Exp. Station Bull. **347**:533–618. *pl. 37. figs. 101.* 1914.

[11] JOHNSON, DUNCAN S., Studies of the development of the Piperaceae. II. The structure and seed-development of *Peperomia hispidula*. Amer. Jour. Bot. **1**: 323–339, 357–397. *pls. 36–38, 41–43.* 1914.

type of embryo sac, as a basis of comparison with the other species to be described later. His topics are as follows: habit and vegetative structure, development of the spike and flower; the stamen, microspore, and pollen tube; the carpel and fruit, ovule and seed; the embryo sac, embryo, and endosperm; germination; and abnormal embryo sacs.

It is a very full and satisfactory presentation of the facts, on the basis of which the following conclusions are reached. In vegetative structure, *P. hispidula* is simpler than any of its relatives, and its delicate herbaceous stem, as well as the accompanying structures, are probably due to recent modification of the more complex type of structure. The flowers are naked, and there is no evidence that they ever possessed a perianth. The megaspore mother cell develops a tetrahedral tetrad of megaspores, whose delicate walls soon disappear, leaving the 4 nuclei in a continuous protoplast. The 4 megaspore nuclei divide to form the characteristic 16-nucleate embryo sac, with its egg and solitary synergid, and its huge endosperm nucleus, formed by the fusion of 14 nuclei. This embryo sac cannot be regarded as primitive, but rather as a compound sac, a structure unknown among the simpler forms. The restriction of the function of the endosperm to that of a "nurse" for the embryo, the food supply being stored in the perisperm, is regarded as "the next to the last step in the disappearance of the endosperm," which becomes practically complete in the Helobiales, Orchidaceae, etc.

To the reviewer, this study is a most satisfactory illustration of the fact that many conditions which appear primitive upon superficial examination may prove upon real examination to be derived and specialized conditions. —J. M. C.

Peridium formation in the aecium.—KURSSANOW[12] adds several interesting details to former accounts of the process by which the layer of peridial cells is formed over the outer surface of the developing mass of aeciospores. It had formerly been held that no intercalary cells were formed in the peripheral chains that constitute the lateral walls of the peridium, and that the peridial cells that make up these chains were metamorphosed aeciospore initial cells that had failed to divide. KURSSANOW finds, however, that intercalary cells are normally produced in these peripheral chains as well as in the interior aeciospore chains. They are not intercalary in position, but are cut off at the lower outer corner of the initial cell when this cell is about the third from the base of the chain. They enlarge somewhat after their abstriction, but soon become disorganized and form a structureless, gelatinous layer between the outer wall of the peridium and the sterile tissue that surrounds it. The production of intercalary cells was more readily followed and the cells were more persistent in the deep-seated, cylindrical aecia of *Puccinia graminis* and *Gymnosporangium tremelloides* than in any of the other 8 species with cupulate

[12] KURSSANOW, L., Über die Peridienentwicklung im Aecidium. Ber. Deutsch. Bot. Gesells. **32**:317–327. *pl. 6. figs. 2.* 1914.

aecia that were studied. In agreement with others he finds that the cells of the central arch of the peridium are the apical cells of the central spore chains that have, before their metamorphosis into peridial cells, cut off intercalary cells below. All of the cells of the peridium are therefore morphologically aeciospores. An apparent exception to this was found in *Peridermium Pini*. In the division of the peridium initial cells of the central arch the usual process is reversed and the small intercalary cell is cut off above and the peridial cell below. A brief description of the fertilization processes in this species is given. Equal cell fusions similar to those first described by CHRISTMAN were found.—F. D. FROMME.

Reciprocal crosses of Oenothera.—DAVIS[13] has reported a partial confirmation of the results obtained by DE VRIES from reciprocal crosses between *Oenothera biennis* L. and *O. muricata* L. The observations of DAVIS also include reciprocal crosses between *O. biennis* L. and *O. franciscana* Bartlett, between *O. biennis* and *O. grandiflora* Solander, and between *O. muricata* L. and *O. gigas* De Vries. Detailed, parallel descriptions are given of the parents and of the pairs of reciprocals, together with numerous photographs of the plants in various stages of their growth. Except in the case of the *gigas-muricata* crosses, the reciprocals of which were in general without important distinguishing characters, the reciprocal crosses exhibited striking contrasting differences. In most respects the crosses closely resembled the pollen parent (patroclinous), as had been noted earlier by DE VRIES for one of these crosses, but strong matroclinous tendencies were also observed, particularly in certain features of the inflorescence of the *biennis-muricata* crosses. Red coloration was found to be wholly or partially dominant without respect to whether it was contributed by the paternal or maternal parent. Moreover, in all the crosses observed by DAVIS, even where patroclinous and matroclinous tendencies were most conspicuous, the influence of both parents was plainly recognizable. He has "observed no certain evidence that a morphological character of either species in a cross is passed on to the F_1 hybrids exactly as it is represented in one or the other of the parents." This fact, DAVIS notes, would render untenable GOLDSCHMIDT'S assumption of merogony, even though that explanation had not been made doubtful by the cytological data of RENNER. No satisfactory explanation of these results has been suggested.—R. A. EMERSON.

Transpiration in succulent plants.—DELF[14] has made an interesting study of the transpiration peculiarities of the different classes of succulent plants, having carried on a number of experiments and having endeavored to organize

[13] DAVIS, BRADLEY MOORE, Genetical studies on *Oenothera*, V. Zeitsch. Ind. Abst.- u. Vererbungslehre **12**:169–205. 1914.

[14] DELF, E. MARION, Transpiration in succulent plants. Ann. Botany **26**:409–442. 1912.

in a systematic way the very chaotic literature of the subject. It is concluded that the chief structural features of these plants are connected with the transpiring surface and the accumulation of water. As to the transpiring surface, there is a greater or less amount of reduction, supplemented in many cases by features that tend to diminish transpiration, such as protected stomata, aerial water absorption, wax coats, etc. The formation of the water tissue that is so characteristic of succulents seems to be "related to the production of organic acids, owing to the influence of limited gaseous exchange on metabolism, and to the presence of chlorides or sulphates in excess in the soil water." DELF agrees with HOLTERMANN that these considerations do not fully explain succulence, since some plants (as *Salicornia*) are so far modified as to be obligate halophytes, whereas other plants (as *Aster Tripolium*) are facultative halophytes, and still others (as *Suaeda fruticosa*) can endure either saline or non-saline habitats without appreciable structural change. In some cases succulence is a hereditary feature, whereas in others it is related to the conditions experienced by the individual showing it. The author believes that water tissue in all cases is of advantage in allowing a plant to "support a rate of water loss which is very considerable, relative to the transpiring surface."—H. C. COWLES.

The vegetation of Clare Island, Ireland.—A paper by R. L. PRAEGER on the vascular plants of Clare Island is but one of a large series of papers, published as Volume 31 of the Proceedings of the Royal Irish Academy.[15] The total number of papers or parts is 68, thus representing probably the most complete natural history survey ever made of any district in the world. The work has been carried on by more than a hundred specialists. The thoroughness with which the work has been done is well illustrated by the fact that in 18 papers there are recorded nearly 700 species of plants and animals not previously found in Ireland, 60 not previously found in the British Isles, and 17 species that are new to science.

Clare Island is an exposed headland, embracing six square miles, and situated three miles from the mainland. The highest point is 1500 feet above the sea. The number of vascular plants indigenous to the island is under 400. The dominating vegetation type is moorland, which includes practically everything over 200 feet. On the precipitous Croaghmore cliff, 1500 feet high, there is a remarkable alpine colony of 10 species, some of which come down almost to sea-level. There is a detailed and interesting discussion of the origin of the flora. Attention is given to the possibility of a land bridge. Wind and birds are regarded as more important than water as dispersing agents.

[15] PRAEGER, R. L., Phanerogamia and Pteridophyta. Clare Island Survey; a scientific survey of Clare Island, in the county of Mayo, Ireland, and of the adjoining parts of the mainland. Proc. Roy. Irish Acad. 31^{10}: 1–112. *pls.* 6. 1911. The entire series can be secured for 60*s.* from the Secretary, Royal Irish Academy, Dawson St., Dublin.

It is noted that a good deal depends on the efficiency of accidental or occasional dispersal.—H. C. COWLES.

The origin of Monocotyledons by self-adaptation.—A great many years ago, HENSLOW proposed the strange theory that Monocotyledons have arisen from Dicotyledons through self-adaptation to an aquatic habitat. Recently he has published[16] further along similar lines; now, however, he regards the notion as a fact instead of a theory, although his line of reasoning is practically unaccepted and is quite out of harmony with the views of modern morphology and ecology. His argument is based on the unsound premise that such formative reactions as those of amphibious plants to water lie at the root of the evolutionary process. No one knows what lies at the root of the evolutionary process, but it is rather certain that it is not this. Water is regarded as causing degeneracy in form and structure, and aquatic seed plants are regarded as degraded land plants. Monocotyledons are supposed to have arisen from Dicotyledons by such degeneracy; non-aquatic Monocotyledons have merely crawled back again upon the land, though retaining their degenerate features. Other authors have regarded Monocotyledons as degenerate Dicotyledons, but self-adaptation as a cause of degeneracy has rarely been postulated; indeed the two ideas, self-adaptation and degeneracy, to the reviewer seem mutually contradictory. A form that is plastic and becomes suited to its environment should not be called degenerate, even though certain organs are reduced or even lost.—H. C. COWLES.

Anatomy of the node.—SINNOTT[17] has concluded that the anatomy of the node may be of great service in indicating the relationships of angiosperms. He considers the "trilacunar" type of node as probably the most ancient available type, meaning that there is a foliar supply of three bundles, each causing a gap of its own in the stem cylinder. This type is characteristic of the Amentiferae, and is present in the majority of Ranales and Rosales. Derived by reduction from this type, as indicated by the study of transitional families, is the "unilacunar" type, characteristic of all the Centrospermae and also of numerous families of the Archichlamydeae and Sympetalae. There is also a "multilacunar" type, derived by the "amplification" of the primitive trilacunar type, which reaches its highest development in Polygonales and Umbellales.

In developing the facts, SINNOTT has examined about 400 genera, distributed among 36 orders, and gives a list of families with their number of nodal

[16] HENSLOW, G., The origin of Monocotyledons from Dicotyledons through self-adaptation to a moist or aquatic habit. Ann. Botany **25**:717–744. 1911; see also Jour. Roy. Hort. Soc. **37**:88–94, 289–294. 1911.

[17] SINNOTT, E. W., Investigations on the phylogeny of angiosperms. I. The anatomy of the node as an aid in the classsification of angiosperms. Amer. Jour. Bot. **1**:303–322. *pls. 30–35.* 1914.

gaps. He feels justified in expressing the opinion that nodal anatomy will take an important place in the final construction of the phylogeny of angiosperms.—J. M. C.

Marine algae of Peru.—HOWE[18] has published an account of the marine algae of Peru, based chiefly upon collections made by Dr. ROBERT E. COKER while acting as fisheries expert to the government of Peru during the years 1906–1908. The list includes 96 species, 29 of which are described as new. Among the latter is a new genus of Rhodophyceae (*Lobocalyx*), referred to Nemalionaceae. The distribution among the great groups is as follows: Cyanophyceae 7, Chlorophyceae 20, Phaeophyceae 15, Rhodophyceae 54. The economic importance of the marine algae, recently emphasized by investigations carried on by the United States Department of Agriculture, is referred to in this report. Attention is called to the fact that *Macrocystis* and the other large seaweeds (as *Lessonia* and *Eisenia*) are abundant on certain parts of the coast of Peru, and that they may prove important as a source of "potash."—J. M. C.

Liverworts of Peru.—The Yale Peruvian Expedition of 1911 collected 31 species of Hepaticae in a condition to be identified, 14 genera being represented. Of three thallose species, two belong to Marchantiales. According to EVANS,[19] six species are new: one in *Metzgeria*, four in *Plagiochila*, and one in *Lejeunea* (*Dicranolejeunea*). Apparently all of this material is desiccated and therefore unfit for critical morphological study. It is unfortunate that even at the present day most collectors do not realize the importance of properly preserved material. In the naming of some of these new species "honor" is conferred upon different individuals. It is to be hoped that taxonomists of the future will use descriptive names so far as possible when describing new genera and species.—W. J. G. LAND.

Lepidostrobus.—MRS. ARBER[20] has published an anatomical study of *Lepidostrobus*, which brings together our previous knowledge of the genus and adds some unrecorded features. Perhaps the most noteworthy new feature is the presence of a sterile plate in the sporangia of *L. Oldhamius* and *L. foliaceus*. This delicate radial plate arises from the floor of the sporangium, and dies out toward the distal end. Two new species are described, *L. Binneyanus* and *L. gracilis*, and also two new forms of *L. Oldhamius*.—J. M. C.

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[18] HOWE, MARSHALL AVERY, The marine algae of Peru. Mem. Torr. Bot. Club **15**: 1–185. *pls. 1–66.* 1914.

[19] EVANS, ALEXANDER W., Hepaticae. Yale Peruvian Expedition of 1911. Trans. Conn. Acad. Sci. **18**: 291–345. *figs. 11.* 1914.

[20] ARBER, AGNES, An anatomical study of the paleozoic cone genus *Lepidostrobus*. Trans. Linn. Soc. London II. Bot. **8**: 205–238. *pls. 21–27.* 1914.